The effect of supplementary nectar feeders on bird-plant mutualisms in the Cape Fynbos, South Africa

by
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Plagiarism declaration

I, Monique du Plessis, know the meaning of plagiarism and declare that all of the work in the dissertation, save for that which is properly acknowledged, is my own.

Signed by candidate

Monique du Plessis
November 2020

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Abstract

Across the world, people feed birds to interact with nature. A variety of feeder types have been developed over the years to target a broad bird community. Attracting nectarivorous birds to gardens using supplementary nectar feeders is a popular human activity across the globe, but few studies have explored its effects on birds and the plants they pollinate. Nectar feeders may have positive effects, facilitating the urban adaptation of nectarivorous birds, and supplementing their diets when floral resources are scarce. However, supplementary feeders may also lure birds away from indigenous vegetation, affecting the rate of visits to bird-pollinated plants, with consequences for seed set. This study is the first to investigate the effect of nectar feeders on an African plant-pollinator mutualism.

Given that many plant species in the fynbos biome are bird pollinated, this study was conducted in residential gardens and natural vegetation along the urban edge of the Cape Peninsula, South Africa. I carried out a feeding experiment with a matched paired design to answer two main questions: (1) Do nectar feeders affect bird abundance and distribution ranges? If so, (2) do these affect their visitation rates to bird-pollinated plants? I conducted bird surveys to compare relative bird abundance and local distribution patterns for three feeding guilds (i.e., nectar-specialists, nectar-opportunists and non-nectarivores) between feeder and control treatments (Chapter 2). I then tested whether the presence of nectar feeders in gardens affected sunbird visitation rates to two bird-pollinated *Erica* species (*Erica plukenetii* subsp. *plukenetii* and *Erica abietina* subsp. *atrorosea*) in the neighbouring vegetation compared to control sites (Chapter 3).

In chapter 2, I found that nectar feeders attracted higher densities of avian nectarivores (but not non-nectarivores) to gardens relative to natural vegetation, and decreased their densities in the neighbouring fynbos, even when floral abundance in the neighbouring vegetation was high. In chapter 3, I found that the consequent changes to sunbird distribution patterns (the main pollinators of ericas) seemed to have no influence on visitation rates to *E. abietina*, but decreased visitation to *E. plukenetii* flowers within 300 m of gardens with feeders.

Thus, nectar feeders may have positive effects for birds themselves by reducing their urban sensitivity but may also have negative effects on the surrounding fynbos ecosystem. Given that nectar feeders appear to compete with the flowers of *E. plukenetii*, and perhaps those of other bird-pollinated species, supplementary feeding may inadvertently threaten bird-plant pollination

networks. This issue is particularly concerning in biomes such as the Cape Floristic Region where many bird-pollinated plants occur near urban edges.

CHAPTER ONE: Introduction

Supplementary bird feeding is a popular garden activity across the world. The practice of bird feeding originated in the northern hemisphere to aid the survival of wild birds during severe winters (Jones and Reynolds 2008; Cox and Gaston 2016). Today, wild birds are fed throughout the year in many countries for various reasons, ranging from personal enjoyment to a sense of moral obligation towards the environment (Jones and Reynolds 2008; Galbraith et al. 2014). Interacting with nature in such a way is thought to promote human well-being and overall health (Galbraith et al. 2014; Cox and Gaston 2016). It is also argued that supplementary feeding has conservation value and is necessary to facilitate certain wild bird populations in urban environments. For example, the British Trust for Ornithology encouraged people in the UK to participate in bird feeding activities, and consequently, the red kite (*Milvus milvus*) population has recolonized the urban areas (Orros and Fellowes 2015a). The large amounts of bird food provided in people's gardens is the primary factor explaining their day-time abundance in these areas.

Given the widespread provisioning of bird food daily, supplementary bird feeding has essentially become an ecosystem-scale intervention, yet its ecological effects remain understudied (Jones and Reynolds 2008; Galbraith et al. 2014). Although seed feeders are most commonly used, supplementary nectar feeders are becoming increasingly popular to attract nectarivorous birds to gardens. Despite the ecological importance of bird pollination, there is little information on the effects of nectar feeders, not only on nectarivorous birds, but also on the plants that depend on their pollination (Arizmendi et al. 2007; McCaffrey and Wethington 2008; Avalos et al. 2012; Brockmeyer and Schaefer 2012; Sonne et al. 2016; Greig et al. 2017; Maguina and Muchhala 2017). From the perspective of enhancing biodiversity in city regions, attracting nectarivorous birds with nectar feeders may, at first glance, appear to be a positive activity as it could increase the capacity of urban areas to support avian pollinators, for example (Coetzee et al. 2018). However, there can also be many unintended consequences associated with it, whether it be negative or positive. There is, for example, some evidence that nectar feeders alter the distribution ranges of hummingbirds (Avalos et al. 2012; Greig et al. 2017), in turn, affecting their pollination rates of bird-pollinated plants (Arizmendi et al. 2007; McCaffrey and Wethington 2008; Brockmeyer and Schaefer 2012; Sonne et al. 2016).

Plant-pollinator mutualisms form crucial components in the web of life (Bascompte and Jordano 2007; Vázquez et al. 2009). More than 87% of all flowering plants rely on animals for reproductive success, and in return reward the pollinators with nectar and pollen (Ollerton et al. 2011). Pollinators forage selectively by choosing to feed on flowers that provide them the greatest reward for the least amount of effort to balance their energy intake relative to expenditure. Consequently, the foraging behaviour of pollinators drives the speciation of angiosperms, and *vice versa* (Fontaine et al. 2006; Gegear and Burns 2007; Pauw 2019).

To promote successful pollination, plants have evolved a suite of traits to advertise their rewards and optimise pollination through a specific pollinator agent, forming apparent pollination syndromes (Faegri and Van Der Pijl 1979). Although pollination syndromes based on floral adaptations alone has been questioned (e.g., Fenster et al. 2004; Ollerton et al. 2009) and is often more generalized than expected (e.g., Wang 2020), it can be used as a starting point to predict pollinator mechanisms. Over 920 bird species across the world are expected to be prominent pollinators (Faegri and Van Der Pijl 1979; Whelan et al. 2008; Şekercioğlu et al. 2016). The bird-pollination syndrome is traditionally characterized by interactions between plants that possess 'ornithophilous' traits and nectarivorous birds. Among these are the hummingbirds (Trochilidae) in North and South America, honeyeaters (Meliphagidae) in Australasia, and the sunbirds (Nectariniidae) and sugarbirds (Promeropidae) in Africa (Cronk and Ojeda 2008). Bird-pollinated (ornithophilous) plants are diverse in colour and morphology, but frequently have tubular, reddish flowers that contain large volumes of dilute nectar and lack scent as an attractant. Their stigma and anthers are suitably orientated to ensure contact with birds while they forage. Correspondingly, avian pollinators have evolved specialized morphological, physiological, and behavioural adaptations that enable them to efficiently access nectar from flowers. Nectar-specialist species have long, narrow bills that are often curved to match the morphology of the flowers they feed on. In some species, a micropump mechanism allows them to easily extract nectar with their tongues as they probe the tubular corolla (Mbatha et al. 2002; Downs 2004; Rico-Guevara et al. 2015). Owing to their dilute nectar diet, nectar-specialists are small, energetic birds with high metabolic rates (Leon and Nicolson 1997; Lotz and Nicolson 2002; Nicolson and Fleming 2003b). To regulate their daily energy intake, nectar-specialist birds can change the frequency at which they feed according to the nectar concentration and volume (Collins and Morellini 1979; Downs 2000). South African nectar-specialists, for example, increase their nectar intake rate when nectar concentration is low (Calf et al. 2003b). Nectar-specialist birds can identify flowers that contain high reward and quality nectar using visual signals and spatial memory as their foraging strategy (Gill and Wolf 1977; Hurly and Healy 1996; Sulikowski and Burke 2012; Whitfield et al. 2014). Although nectar-specialist birds rely mostly on a nectar diet, they obtain the bulk of their protein requirements from feeding on insects, especially during breeding season and periods when nectar availability is low and arthropod abundance is high (Daniels et al. 2001).

Given their strong dependence on nectar, nectarivorous birds readily use supplementary nectar feeders (Coetzee et al. 2018). The sugar solution in nectar feeders is often made to similar concentration and nutritional value as that found in natural flower nectar but offers an advantage over flowers as it provides much greater quantities and predictable sources of food (Coetzee et al. 2020). It is estimated that a single feeder containing approximately 500ml of sugar water can feed at least 10 sunbirds a day (Nicolson and Fleming 2003a). Considering that nectarivorous bird abundance is strongly linked to nectar volume at small spatial scales (Geerts et al. 2020), it would then not be surprising if birds are attracted in high numbers to nectar feeders. Birds can spend less time and energy feeding at feeders than they would if flying between flowers in search of nectar. If birds are satiated by the generous amounts of “unlimited” supplementary nectar supply, they may reduce their visits to natural flowers in the vicinity. In this way, feeders have the potential to outcompete native flowers for bird attention.

Considering that pollinators and the plants they pollinate are highly interdependent (Pauw 2019), bird-plant pollination systems can be particularly sensitive to anthropogenic interventions (Cronk and Ojeda 2008). Attracting birds with supplementary nectar sources could be considered such an intervention if it affects the foraging and movement ecology of nectarivorous birds. According to the keystone mutualist hypothesis, severe declines in keystone pollinator density or richness may have dire cascading effects on all species involved in the mutualism (Cox et al. 1991; Christian 2001). This is because the functional extinction of avian pollinators can lead to pollinator-limited seed set and subsequently plant reproductive failure (Aguilar et al. 2006; Mortensen et al. 2008; Anderson et al. 2011; Geerts and Pauw 2012; Thomann et al. 2013; Regan et al. 2015; Geerts 2016). Declines in plant fecundity may eventually lead to decreasing plant biomass (Anderson et al. 2011) and changes in plant species composition towards, for example, anemophilous (wind-pollinated) plant species. In extreme cases, this could place the local bird-pollinated plant populations at an extinction risk. Self-incompatible plant species with specialized pollination systems may be especially prone to local extinction if their pollinators are offered alternative food sources. This is because substitute pollinators are unable to effectively contribute to their pollination (Geerts and Pauw 2012; Geerts 2016) and they lack compensatory traits, such as autonomous self-fertilization or vegetative persistence, to buffer against local pollinator loss (Bond 1994; Thomann et al. 2013). Thus, it is vital to understand the responses of nectarivorous bird communities to the presence of nectar feeders as they may interfere with pollination processes, affecting local plant populations.

Previous studies on this topic have mainly been confined to the Americas, assessing the effects of nectar feeders on hummingbird-plant mutualisms. To date, African bird-pollination systems have not been investigated, yet urban areas are anticipated to undergo rapid growth in Africa, threatening habitats and plant populations in many countries. In the fynbos biome of South Africa, a biodiversity hotspot known as the Cape Floristic Region (CFR) (Myers et al. 2000), bird pollination plays a key ecological role because a disproportionally large number of plant species depend on only four nectar-specialist bird species that occur throughout the biome. Approximately 15% of the 680 *Erica* (Ericaceae) species (Rebelo et al. 1985) and 25% of the 330 Proteaceae species in the CFR are potentially bird pollinated (Geerts et al. 2020). Exacerbating the asymmetry, the relatively short-billed Orange-breasted Sunbird (*Anthobaphes violacea*) is the main pollinator of bird-pollinated *Erica* species, whereas many members from the Proteaceae family rely primarily on the long-billed Cape Sugarbird (*Promerops cafer*) for their pollination (Skead 1967; Mostert et al. 1980; Collins 1983; Rebelo et al. 1984, 1985; Fraser and McMahon 1992; Geerts and Pauw 2009; Pauw and Johnson 2017). The Malachite Sunbird (*Nectarinia famosa*) and the Southern Double-collared Sunbird (*Cinnyris chalybea*) inhabit a larger area of southern Africa than the two endemic nectarivores and therefore forage on a wider variety of plant families (Skead 1967; Hockey et al. 2005). Even so, the Malachite Sunbird is the exclusive pollinator of many members from the Iridaceae and Amaryllidaceae families (ca. 37 Cape species) (Geerts and Pauw 2009). The interaction between these birds and the plants they pollinate are therefore relatively specialized, making these fynbos communities especially vulnerable to the potential effects of feeders.

Dissertation structure

This dissertation contains two data chapters (Chapter 2 and 3), which are presented as separate papers. Therefore, repetition of some content, especially methods, is unavoidable. Chapter 4 is the concluding chapter that synthesises the outcomes and implications of Chapters 2 and 3. With the exception of *Erica* nectar concentration and volume data from one of my supervisors, Dr A. Coetzee, data presented in each chapter were collected by myself and SANBI research assistants (UCT Ethics Approval Number: 2019/V12/AC; SANParks Permit Number: CRC/2018-2019/020--2016/V1; Cape Nature Permit Number: CN44-28-9368). I carried out all data analysis, with input from my supervisors and consultants from the Department of Statistical Sciences (University of Cape Town).

Chapter objectives and research questions

Chapter 2: Supplementary nectar feeders affect the abundance and ranges of hummingbird and bat species (Arizmendi et al. 2007; McCaffrey and Wethington 2008; Avalos et al. 2012; Brockmeyer and Schaefer 2012; Sonne et al. 2016; Greig et al. 2017; Maguina and Muchhala 2017). Although there is some evidence that sunbirds make use of nectar feeders in gardens in the Cape Peninsula (Coetzee et al. 2018), it remains to be tested whether nectar feeders affect the relative densities and distribution of nectarivorous birds in the surrounding natural habitat. To address this, I used an experiment with nectar feeders in gardens on the suburban edge of the Cape Peninsula. I carried out bird surveys to compare local bird abundance and relative distribution patterns of three avian feeding guilds (i.e., nectar-specialists, nectar-opportunists and non-nectarivores) between feeder and control treatment sites. I conducted experiments in both the wet winter and dry summer because nectar feeders may be less attractive when floral resources are more abundant compared to when they are scarce. I asked: (1) does the presence of nectar feeders change relative bird densities in gardens and neighbouring natural vegetation compared to gardens without feeders? (2) do nectar feeders alter local scale bird distributions in natural vegetation compared to control gardens without feeders? (3) are these patterns the same for all four nectar-specialist species? and, finally, (4) does the effect of nectar feeders on nectarivorous bird density and distribution vary with season?

Chapter 3: The presence of nectar feeders can affect pollination rates of some hummingbird-pollinated plant species (Arizmendi et al. 2007; Avalos et al. 2012; Brockmeyer and Schaefer 2012; Sonne et al. 2016). Whether nectar feeders facilitate or compete with bird-pollinated plant species for bird attention is still debated, however. Local flowering plants may receive increased visits as birds are drawn into the area, or they may receive reduced visits if nectar feeders outcompete birds for their attention. The effect of nectar feeders on African bird-plant systems has not yet been investigated. Bird-pollinated *Erica* species provide a useful system to test the effect of feeders on pollination, because their visitation rates are relatively easy to measure using their anther ring status (Geerts and Pauw 2011a). In this chapter, I consider the effect of nectar feeders in suburban gardens on the visitation rate of two co-occurring *Erica* species, *E. abietina* and *E. plukenetii*. Specifically, I tested whether sunbird visitation rates to these two species differs between feeder and control treatments, and with distance from the gardens. I therefore monitored their anther ring status during peak flowering season (winter 2019) at different distances from the gardens before and after the feeders were present for a week. I then compared differences in visitation rate between control and feeder treatment groups.

CHAPTER TWO

Do supplementary nectar feeders affect bird communities on the urban edge of the Cape Fynbos, South Africa?

Abstract

Humans feed wild birds to the point where it is essentially a global experiment, yet few empirical studies have tested its effects on bird communities. One type of bird feeding involves the use of supplementary nectar feeders (hereafter, nectar feeders) to attract nectarivorous birds to gardens and supplement their diets when floral resources are scarce. Nectar feeders may have positive effects by attracting nectarivores towards suburban environments, allowing suburbia to provide stepping-stones between fragmented natural areas, and supplementing bird diets when floral resources are scarce. This may facilitate bird adaptation to anthropogenically induced shifts such as climate and land-use change. However, it may also come at the cost of luring them away from the plants they pollinate in neighbouring indigenous vegetation, with consequences for seed set. To date, the effect of nectar feeders on African bird communities have not been studied, despite the rapid growth of urban areas across the continent. This study investigated how nectar feeders affect bird community structures in the Cape Peninsula of Cape Town, South Africa. I carried out a feeding experiment to compare relative bird abundance and local distribution patterns for three avian feeding guilds (i.e. nectar-specialists, nectar-opportunists and non-nectarivores) between feeder and control treatments. Bird surveys were conducted at 18 sites across four residential areas during winter and summer 2019. Twenty-minute point counts were conducted in gardens along the suburban edge and in three plots at different distances up to 150 m into the neighbouring natural vegetation. Feeders affected relative bird abundances and local ranges of nectarivores, but not of non-nectarivores. Feeders increased bird densities in gardens for all four nectar-specialist species, drawing them away from natural vegetation. The attraction to feeders was stronger than the aversion of the suburban environment, even for urban-sensitive specialist species, such as Orange-breasted Sunbirds (*Anthobaphes violacea*). Nectarivorous bird density near feeders was greater than in natural vegetation in both seasons, suggesting that nectarivorous birds use feeders, even during periods of high floral abundance. This study provides evidence that nectar feeders can facilitate the nectarivorous feeding guild in the suburban environment of an African city by reducing their urban sensitivity. However, it also highlights the need to further explore potential indirect effects that nectar feeders may have on the surrounding ecosystem, such as local bird-pollinated plant populations, given that feeders can compete with indigenous flowering species for birds' attention.

Key words: *artificial nectar feeders, avian nectarivores, bird feeding, bird pollination, indirect effects in human-wildlife interactions, sugar water feeders*

Introduction

As humanity becomes increasingly urban and people concentrate in cities with impoverished biodiversity, there is a progressive disengagement with the natural world and people can lose out on the opportunity to benefit or learn from nature (Seymour et al. 2019). However, many people still seek ways in which to interact with nature, and as a result, wild bird feeding has become one of the most widespread forms of wildlife interactions globally (Jones and Reynolds 2008; Orros and Fellowes 2015b; Reynolds et al. 2017). Nearly half of urban households in the United Kingdom (Davies et al. 2009), United States of America (U.S. Fish & Wildlife Service 2013), Australia (Jones and Reynolds 2008) and New Zealand (Galbraith et al. 2014) frequently provide supplementary food to wild birds in their gardens.

Although wild bird feeding is now so widespread that it is essentially a global experiment, surprisingly few experimental studies have assessed how and to what extent it affects bird communities (Jones and Reynolds 2008; Galbraith et al. 2015). Moreover, most studies on supplemental bird feeding are not conducted in actual residential gardens in the urban environment, and so fail to reflect the true conditions (Robb et al. 2008). Due to the lack of knowledge on the effects of supplementary feeding, thousands of people with sincere intentions are providing a wide variety of bird food daily without reliable guidance on how to feed responsibly (Jones 2011). However, these anthropogenic food sources may influence the structure of bird communities at various spatial scales (Fuller et al. 2008; Robb et al. 2008; Jones 2011; Amrhein 2014; Galbraith et al. 2015; Tryjanowski et al. 2015). The evidence so far shows that whilst supplementary feeding can bring positive benefits in certain scenarios (Orros and Fellowes 2015a), there are also numerous potential negative consequences. For example, conservation organizations in Australia discourage people from feeding birds in private gardens and public parks (Jones and Reynolds 2008), with a primary concern being that birds could become reliant on supplementary feeding if food is provided too frequently (Rollinson et al. 2003; Brockmeyer and Schaefer 2012). Conversely, if food is of low quality and/or provided too unreliably, birds can suffer from malnutrition (Wilcoxen et al. 2015; Stofberg et al. 2019). Aggregation of high densities of birds around feeders may also increase avian disease transmission and predation risk (Robb et al. 2008; Jones 2011). Given that pets occur at far higher densities than natural predators (Baker et al. 2005; Sims et al. 2007; Thomas et al. 2012; Seymour et al. 2020), gardens with feeders can act as sinks if predation by pets is high. The presence of pets can also create an atmosphere of fear, leading to reduced reproductive fitness (Bonnington et al. 2013). Moreover, there is evidence that supplementary food can change the composition of bird communities, by favouring exotic bird species (Galbraith et al. 2015, 2017). Finally, supplementary feeders may sometimes alter the natural foraging behaviour of birds, ultimately attracting them away from their natural food sources (Arizmendi et al. 2007; Avalos et al. 2012). However, at certain times the food provision allows the persistence of species in an urban habitat mosaic (Thabethe and Downs 2018). There is therefore some disagreement amongst conservation organisations and members of the public about whether wild bird feeding should be encouraged (Jones 2011).

Although the most common type of bird feeder provides seeds to granivorous passerines, many people provide supplementary nectar feeders to attract nectarivorous birds to gardens. While nectar feeders are used by many bird enthusiasts and researchers during banding studies (Inouye et al. 1991), relatively little is known about their effects on the structure of nectarivorous bird communities. Most research to date has been on hummingbirds and bats in North and Central America (Arizmendi et al. 2007; McCaffrey and Wethington 2008; Avalos et al. 2012; Brockmeyer and Schaefer 2012; Sonne et al. 2016; Greig et al. 2017; Maguina and Muchhala 2017). These studies all found significant increases in hummingbird and bat abundance due to nectar feeders, although there is some debate on the implications of these changes on hummingbird-plant pollination mutualisms. For instance, Avalos et al. (2012) showed that nectar feeders attract high densities of hummingbirds, potentially from as far as 3 km away, leading them away from flowers and reducing the pollen loads carried by birds. In contrast, Sonne et al. (2015) found that nectar feeders may increase local bird abundance but do not necessarily negatively affect pollination mutualisms with nearby plants. Brockmeyer and Schaefer (2012) even reported that feeders may have a positive effect on plant populations by facilitating local flower visitation, though the cost to plants further away remains unknown.

In Africa, a rich community of bird-pollinated plants is pollinated by nectarivores such as sunbirds (Nectariniidae), sugarbirds (Promeropidae) and white-eyes (Zosteropidae). The effect of nectar feeders on these African nectarivorous communities requires attention, especially considering the rapid expansion of urbanization in many developing countries. Cape Town is one of South Africa's fastest growing cities with the lowlands in this area already extensively developed (Rebelo et al. 2011). The city is located in the megadiverse Cape Floristic Region (CFR) where only four resident nectar-specialist birds pollinate over 300 plant species (Rebelo et al. 1984; Rebelo 1987; Myers et al. 2000). It is therefore vital to understand how these nectarivorous birds respond to nectar feeders, because it may have cascading effects on all species involved in the pollination mutualism. An adjustment to bird foraging and movement ecology could potentially interfere with plant-pollinator networks already under pressure from many anthropogenic effects, with implications for the surrounding ecosystem. Moreover, nectarivorous birds drive the evolution of bird-pollinated plants, while bird-pollinated plants, in turn, influence the evolution of the nectarivorous birds (Pauw 2019), such that nectar feeders may disrupt the action of selection on both parties.

Four specialist nectarivorous bird species are common residents in the CFR: the endemic Orange-breasted Sunbird (*Anthobaphes violacea*) and Cape Sugarbird (*Promerops cafer*), as well as the more widespread Malachite Sunbird (*Nectarinia famosa*) and Southern Double-collared Sunbird (*Cinnyris chalybea*). Although these nectarivores are abundant in fynbos vegetation, the Cape Town suburban environment reduces nectarivore functional diversity: it presents an impermeable barrier to the Orange-breasted Sunbird and Cape Sugarbird, and reduces movement of the Malachite Sunbird (Pauw and Louw 2012). Only the short-billed Southern Double-collared Sunbird occurs throughout the urbanized landscape, but is unable to successfully pollinate many of the longer-tubed flowers in this region (Geerts and Pauw 2009; Geerts 2016). Pauw and Louw (2012) suggested that nectar feeders could restore the functional diversity of this guild of pollinators throughout the city, creating stepping-stones by attracting otherwise urban-sensitive nectarivores towards the interior of the urban landscape. Coetzee et al. (2018) provides the first published evidence that nectar feeders can facilitate the existence of all four specialist nectarivores in Cape Town. Yet, Coetzee et al. (2018) mainly used questionnaires to determine the presence and absence of birds in gardens and did not investigate how bird densities changed in the surrounding natural vegetation. Therefore, further empirical evidence is required to gain an accurate understanding of not only whether nectar feeders attract birds to gardens, but how they affect local bird distribution in the Cape Fynbos.

Although nectar feeders target specialist nectarivores, they are likely to also attract generalist species that include nectar in their diets, of which there are many in the CFR (Supplementary Information A: Table S1). These species also generally contribute to the pollination of flowers with floral structures more available to generalist bird pollinators (Rebelo 1987; Botes et al. 2008; Brown et al. 2009; Arena et al. 2013). Nectar feeders may even affect birds that do not include nectar in their diets through competition, for example for nesting sites or foraging sources shared with non-specialist nectarivores (Galbraith et al. 2015; Orros et al. 2015). Therefore, to fully understand the effects of nectar feeders on local bird communities, it is important to assess all feeding groups.

The relative attraction of nectar feeders may differ with season. When flower nectar is relatively abundant in natural vegetation, nectar feeders may be less attractive (Inouye et al. 1991), and *vice versa*. For example, hummingbirds prefer feeding on flowers over nectar feeders during periods of high floral abundance and only use feeders as an alternative food source (Inouye et al. 1991; McCaffrey and Wethington 2008). The Cape Fynbos experiences dry summers and receives rain in the winter, such that bird-pollinated floral abundances are lower in summer (Rebelo et al. 1984). It is therefore possible that the effects of nectar feeders on bird abundance and distribution are more marked during summer than winter.

Here, I carried out a field experiment to determine whether and how supplementary nectar feeders affect the presence of local bird communities along the urban edge of the Cape Fynbos. I asked: (1) do nectar feeders change relative bird densities in gardens and neighbouring natural vegetation compared to control gardens without feeders? (2) do nectar feeders alter local scale bird distributions in natural vegetation compared to control gardens without feeders? (3) are these patterns (addressed in question 1 and 2) the same for all four nectar-specialist species? and, finally, (4) does the effect of nectar feeders on nectarivorous bird density and distribution vary with season? I hypothesized that nectar feeders influence bird communities in the suburban environment by attracting higher densities of nectarivores (both specialist and opportunistic species) to gardens with feeders compared to gardens without. The attraction to feeders may be stronger than the aversion of the suburban environment, attracting more nectarivores towards gardens than natural vegetation. I therefore expected higher densities of nectarivores in feeder gardens relative to natural areas where they mainly rely on flower nectar for their dietary requirements (French et al. 2005). Specifically, I hypothesized that nectar feeders attract nectarivores away from the neighbouring natural vegetation. It is possible that nectar feeders can encourage birds to overcome their sensitivity to urban environments, as they provide a “bonanza” resource. I therefore expected all four nectar-specialist nectarivores to follow the distribution patterns mentioned above, despite some being considered sensitive to the urban landscape. In contrast, I expected non-nectarivorous bird species to either remain unaffected by the presence of nectar feeders in gardens, or alternatively, be negatively affected by feeders through competitive exclusion. The latter predicts a decrease in non-nectarivorous bird densities in feeder gardens. Finally, I hypothesized that the effects of nectar feeders on nectarivorous bird density and distributions varies seasonally. I expected feeders to attract higher densities of nectarivores during summer, when bird-pollinated floral abundance is relatively low in the natural vegetation, than in winter.

Methods

Study area

The City of Cape Town is situated in the southwest of the biodiverse Cape Floristic Region (CFR) in the Western Cape Province, South Africa (Rebelo et al. 2011). The Cape Fynbos, an important component of the CFR, is home to many endemic plant species, and recognized as a biodiversity hotspot (Holmes et al. 2012). Two of the most prominent groups in fynbos vegetation are fire-prone shrubs from the Proteaceae family and *Erica* genus, and are two of the main food sources for nectarivorous birds. This biodiversity is under severe threat, however, as Cape Town is rapidly growing to engulf remnant natural areas within and bordering the city (Rebelo et al. 2011).

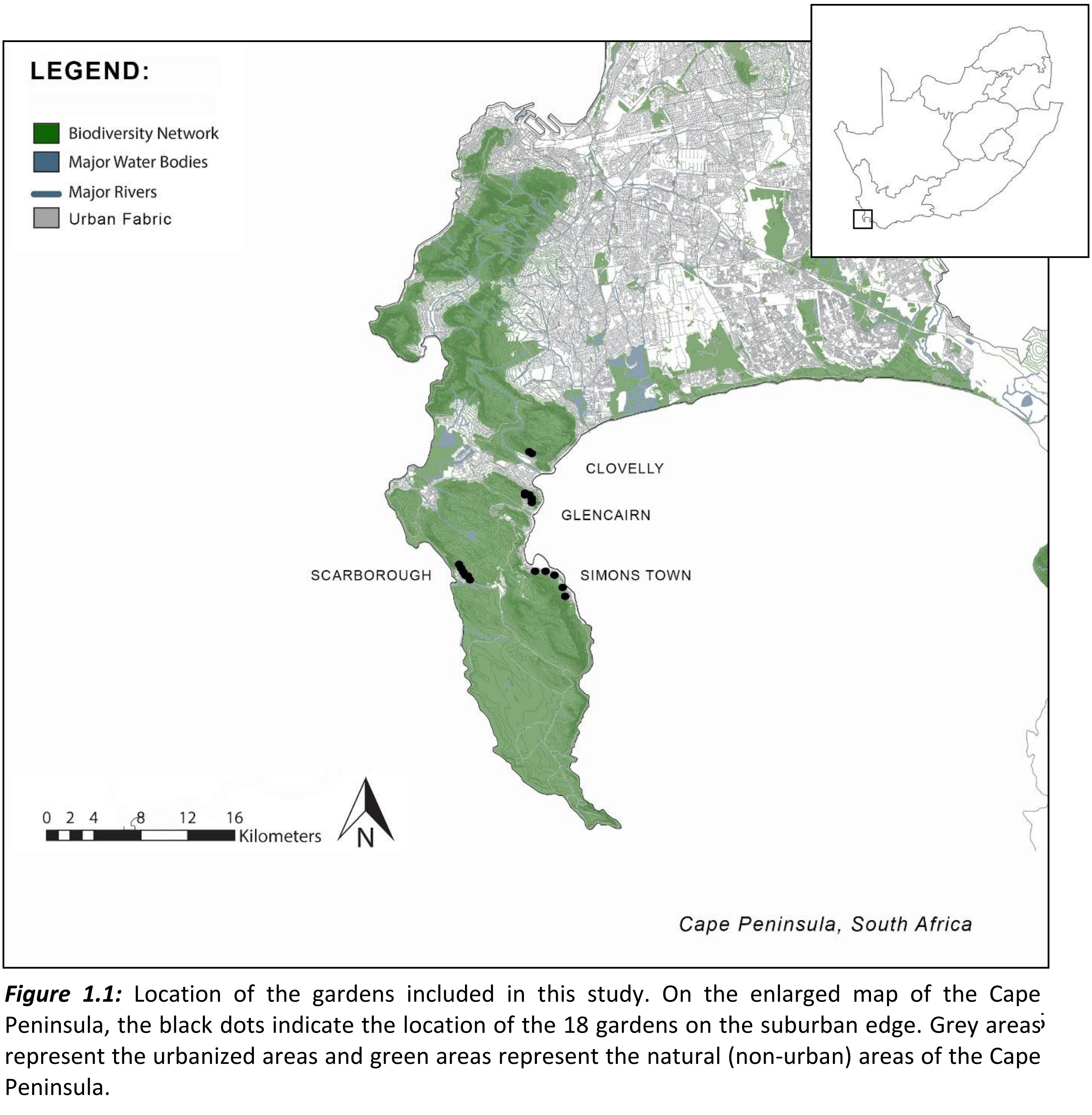

Figure 1.1: Location of the gardens included in this study. On the enlarged map of the Cape Peninsula, the black dots indicate the location of the 18 gardens on the suburban edge. Grey areas represent the urbanized areas and green areas represent the natural (non-urban) areas of the Cape Peninsula.

This study was conducted on the Cape Peninsula south of the city centre of Cape Town (Figure 1.1). Experiments took place in the residential areas of Scarborough, Simon's Town, Glencairn and Clovelly, where nectar feeders are often available in gardens (Coetzee et al. 2018). I conducted experimental trials at 18 sites across the four areas, each defined as a residential garden on the suburban edge and its bordering natural vegetation. These were typically separated by a fire break (~ 10 m wide) along the boundary between the suburban edge and natural vegetation. At each site, plots in which birds were surveyed included one plot in the garden itself, and three plots in the neighbouring natural vegetation running along a transect perpendicular to the garden/natural vegetation boundary at approximately 50 m, 100 m, and 150 m from the gardens. Of the 18 sites, six were in Scarborough, five in Simon's Town, five in Glencairn, and two in Clovelly. The four suburbs are at least four kilometres apart, and gardens within areas were at least 250 m apart to try to ensure independence of visiting birds.

Sites were selected by carrying out door-to-door visits. Twelve gardens were situated directly bordering the fire break on the suburban edge. Two gardens directly bordered natural vegetation, but the fire break lay between the 100 m and 150 m plots. The four remaining gardens were located on the opposite side of the road to the suburban edge, separated by one other house from the natural vegetation border. Garden sizes varied between 52 and 650 m^2, while the survey area of the plots in the natural vegetation were fixed at 40 x 40 m (1600 m^2) each. Therefore, garden and plot size, as well as other garden variables, such as the floral abundance of bird-pollinated plants, presence of pets on the property, and previous presence of private bird feeders, were included in analyses to account for their effects on bird abundance (see Statistical Analyses section for details). Private bird feeders were removed at least one month prior to and during the experiments. Floral abundance in gardens and vegetation was estimated as the total number of all healthy, mature flowers of any bird-pollinated species, not just the two focal *Erica* species in this study, or inflorescences (e.g., bird-pollinated *Protea* species). Note that avian nectarivores sometimes visit open mouthed *Erica* species which are usually extensively visited by insects (Rebelo et al. 1985), but these were not abundant in my study site and were therefore not accounted for in this study.

Study species

Birds are key pollinators of a variety of plant species in the CFR. A number of these birds opportunistically feed on nectar while four are specialist nectarivores: the Cape Sugarbird, Orange-breasted Sunbird, Malachite Sunbird and Southern Double-collared Sunbird. These specialists have long curved bills adapted for drinking nectar from a suite of plant species, many of which have long tubular flowers, facilitating pollination in the process (Skead 1967). Approximately 15% of the 680 *Erica* species in the Cape Fynbos are pollinated by birds in this way (Rebelo et al. 1985). The Orange-breasted Sunbird is almost exclusively associated with many of these bird-pollinated *Erica* species (Rebelo et al. 1984), and the particularly long-billed Malachite Sunbird is the exclusive pollinator of many longer-tubed flowers from the Iridaceae and Amaryllidaceae families (Geerts and Pauw 2009), while the Cape Sugarbird pollinates many members of the Proteaceae family (Rebelo et al. 1984). The Amethyst Sunbird (*Chalcomitra amethystina*), a scarcer species on the Cape Peninsula and more typical of forest edges, was not recorded during this study.

All bird species present during bird surveys were recorded and categorized into one of three feeding guilds (see Supplementary Information: Figure S1.1). I classified "nectar-specialist" species as those for which nectar is their primary food source, and "nectar-opportunists" as species that include nectar in their diets but for which nectar is not a primary food source (these two categories were collectively referred to as "nectarivores") (Hockey et al. 2005). The remainder of species in this study were considered "non-nectarivorous".

Bird surveys

I carried out a seven-day feeding experiment at the 18 sites to investigate the effect of supplementary nectar feeders on the local bird community (Figure 1.2). A recent study on hummingbirds (Nuñez-Rosas and Arizmendi 2019) and a pilot study showed that nectarivores usually respond to feeders within two days after feeder placement, so seven days was considered sufficient time for these surveys. I carried out an experimental and a control trial at each site during each season (winter and summer), yielding a total of four trials per site. To assess whether nectar feeders influence bird distributions, I conducted bird surveys in gardens and the three natural vegetation plots (i.e., at 50 m, 100 m and 150 m from the gardens), placing feeders in some gardens to create "feeder" and "control" treatments. The two treatments were allocated to gardens randomly so that, initially, 10 of the 18 gardens received feeders, and eight did not. The following month, gardens received the opposite treatment. Feeder treatments consisted of four feeders to increase the chance of its detection by birds and to reduce bird competition. Each feeder was filled with a 20% (weight/weight) sucrose solution, similar to the average concentration found in South African bird-pollinated plants which specialist avian nectarivores prefer (20-25% w/w) (Nicolson and Fleming 2003). Feeders were positioned in clusters to form a concentrated source of nectar, and always placed close to a shrub or tree so that the birds could use these as refuges while awaiting their turn at the feeder (see Supplementary Information: Figure S1.1). Feeders were refilled as regularly as

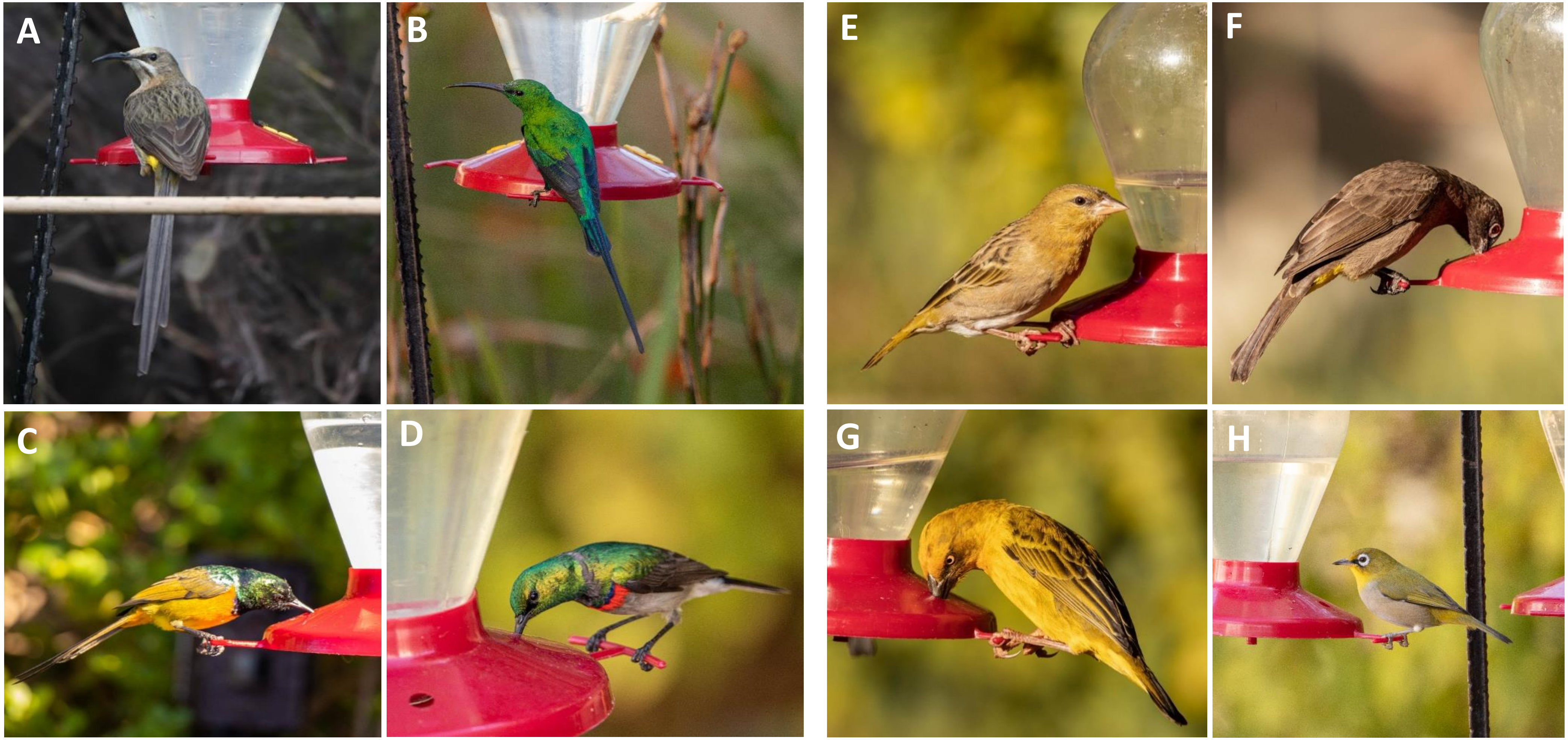

Figure 1.2: Nectarivorous species feeding at supplementary nectar feeders in gardens on the suburban edge of the Cape Peninsula. Nectar-specialist nectarivorous bird species: A) female Cape Sugarbird (*Promerops cafer*), B) male Malachite Sunbird (*Nectarinia famosa*), C) male Orange-breasted Sunbird (*Anthobaphes violacea*), and D) male Southern Double-collared Sunbird (*Cinnyris chalybea*). Nectar-opportunistic species: E) female Southern Masked Weaver (*Ploceus velatus*), F) Cape Bulbul (*Pycnonotus capensis*), G) male Cape Weaver (*Ploceus capensis*), and H) Cape White-eye (*Zosterops virens*). Feeders were filled with a colourless 1:4 sugar to water solution (Images by Monique du Plessis).

needed during the seven days to ensure a continuous supply of sugar water and cleaned thoroughly between trials to minimize transmission of pathogens.

The observer was stationed at a single point on the property or in the veld that provided the widest view of the garden or plot survey area. In natural vegetation, plots were 40 m x 40 m, so that birds were easily seen and heard. Movements were kept to a minimum to avoid affecting bird behaviour while birds and their abundance were surveyed for 20 min. Bird abundance was recorded as the maximum number of individuals per species identified at one time within the restrictions of the garden or plot boundaries, to ensure that individual birds were not counted twice.

Bird surveys started on the fourth day after placing the feeders so that birds had enough time to acclimatize to their presence. Feeders then remained in the garden for another two days and bird surveys were repeated on the seventh day. These repeat counts were to reduce the influence of circumstantial effects on bird activity, e.g., people walking by or unfavourable weather conditions. Very wet, hot (temperature > 30˚C) or windy days (wind > 11 $m.s^{-1}$) were avoided, and a hand-held Kestrel 3000 weather meter (Nielsen-Kellerman Co., Boothwyn, Pennsylvania) was used to record weather conditions. Bird surveys were conducted during peak bird activity hours in the mornings (i.e., one to four hours after sunrise) and afternoons (i.e., from four hours before sunset).

To test whether birds are more likely to visit bird feeders in dry periods when floral abundance is low (Rebelo et al. 1984; Inouye et al. 1991), I ran the experiments during both the wet winter (from May to June, repeated in July 2019), when flower abundance is high, and the dry summer (November, repeated in December 2019), when floral resources are relatively scarce.

Statistical analyses

All data exploration and analyses were conducted in R software (R Core Team 2019). The three feeding guilds were analysed separately, and a separate analysis was conducted on specialist nectarivores to explore species-specific responses to nectar feeders. During data exploration, I used the DHARMa package (Hartig 2019) to test for overdispersion and zero-inflation. Poisson, Negative Binomial or zero-inflated error distributions can all be appropriate for count data given its non-normality, overdispersion and likelihood of high levels of zeros. Therefore, I followed an information-theoretic approach using differences in the Akaike Information Criterion (AIC) (Burnham et al. 2011) to compare and determine the most appropriate error structures for the three feeding guilds and the nectar-specialist species (see Supplementary Information: Table S1.2 for details).

I generated a set of 15 models for each feeding guild and the nectar-specialist species dataset to determine which variables, or combinations of variables, best predict their abundances.

Generalized linear mixed models (GLMM) were fitted with bird abundance as the dependent variable. For each feeding guild, the following variables were included as explanatory variables: treatment, distance, wind speed, season, floral abundance, time of day, presence of previous feeder and pets (see Table 1.1 for details). One of the main goals of this study was to test whether different treatments (feeder vs. control) resulted in different spatial distributions of each feeding guild. This predicted a significant interaction between treatment type and distance from the gardens. Additionally, I aimed to test whether these effects differ with season, which predicted a significant three-way interaction between treatment, distance, and season. Therefore, each model in the model set contained a different combination of distance, treatment, and season, while the remaining independent variables were held constant (see Supplementary Information: Table S1.3 for the full model set). I accounted for the presence of previous feeders because it had a significant negative influence on nectarivorous bird abundance (see Supplementary Information: Table S1.3 for the full model set & Table S1.5 for detailed statistics). Thus, fewer birds visited gardens where feeders were previously maintained, possibly because birds had already established a dominance hierarchy, limiting the maximum number of birds as aggressive individuals exclude others from their territories. I also included the presence of pets on the property as an explanatory variable given its significant negative effect on at least non-nectarivorous birds, likely because they create an atmosphere of fear, deterring them away from gardens. For the separate nectar-specialist species dataset, the following variables were included as explanatory variables: treatment, distance, species, wind speed, season, floral abundance, time of day, presence of previous feeder and pets. My aim with this dataset was to test whether nectar feeders only affect some of the specialist species' abundance and distribution but not others. This predicts a significant three-way interaction between treatment, distance, and species type. Therefore, each model in the model set contained a different combination of treatment, distance, and species (see Supplementary Information: Table S1.4 for the full model set).

In all models for all datasets, site was included as a random effect with random intercept, to account for multiple sampling per site. To correct for the differences in the size of areas surveyed, I included the logarithm of the size of each garden and survey plot as an offset in the model formula. Differences in gardens (e.g., vegetation structure and height) was accounted for by the pairwise design and by having garden ID as a random factor. Continuous independent variables (i.e., distance, wind, and floral abundance) were standardized so that they were on similar scales. I used the lme4 package (Bates et al. 2015) to fit Poisson models and the glmmTMB package (Brooks et al. 2017) for Negative Binomial models (see Supplementary Information: Table S1.2), both using a log link function. An observation-level random effect was included in Poisson models to correct for overdispersion (Browne et al. 2005). I ranked the candidate models using Bayesian Information Criterion (BIC) and BIC weights (w_i) (Burnham et al. 2011) with the MuMIn package (Barton 2012). The BIC is preferred above the AIC in this case, given the relatively large sample sizes for each dataset, because it penalizes the number of parameters more strongly. The weights indicate the percentage support for a model relative to all other candidate models, and the model(s) with delta BIC values lower than two and highest weight was considered as the best model. To assess the goodness-of-fit for each best model, I used the r.squaredGLMM function in the MuMIn package (Barton 2015) to calculate the marginal (R^2m) and conditional pseudo-R^2 values (R^2c), which indicate the variation in the data explained by fixed effects, and by both fixed and random effects, respectively (Nakagawa and Schielzeth 2013). Multi-collinearity tests using Variance Inflation Factors (VIFs) showed that none of the predictor variables had strong relationships (VIFs < 3).

Table 1.1: A list of response and predictor variables used during model selection to test the effect of supplementary nectar feeders on bird abundance and bird distribution along the urban edge of the Cape Peninsula.

Variable	Data Type	Range	Units
Response variable			
abundance	numerical	0–11	maximum number of birds per species during a survey
Predictor variables			
Treatment	categorical	feeder/ control	
Distance	numerical	0=garden/ 50=50 m plot/ 100=100 m plot/ 150=150 m plot	distance from garden (m)
Wind	numerical	0–11	$m.s^{-1}$
Season	categorical	winter/ summer	
Time	categorical	morning/ afternoon	
Previous feeder	logical	TRUE/ FALSE	
Pets	logical	TRUE/ FALSE	
Floral abundance	numerical	0–8000	estimated number of inflorescences/flowers from bird-pollinated plants in each garden and plot
Species	categorical	Orange-breasted Sunbird / Malachite Sunbird, Southern Double-collared Sunbird / Cape Sugarbird	
Random factor			
Site	categorical	1–18	
Offset term			
Size	numerical	52 – 1600	size of gardens and survey plots in the natural vegetation (m^2)

Results

The generalized linear mixed-effect models revealed that nectar feeders affected the relative abundance and distribution of both nectar-specialist and nectar-opportunistic nectarivores, but not that of the non-nectarivores (Table 1.2). The effect of nectar feeders on nectar-specialists and nectar-opportunists did not differ with season. Detailed results for each feeding guild are presented below.

Table 1.2: The top five models for each of the three feeding guilds testing for the effect of supplementary nectar feeders on their local abundance and distribution along the urban edge of the Cape Peninsula. Generalized linear mixed-effect models were constructed, with site as a random factor and the log of size of the survey plots as an offset. For each model, the number of parameters (K), log likelihood (L), Bayesian Information Criterion (BIC), difference in BIC (ΔBIC) from the best model and BIC weight (w_i) is presented. Asterisk (*) indicates both the interaction term and main effect. For each feeding guild, 564 observations were made.

Rank	**Variables in model** [a]	**K**	**L**	**BIC**	**ΔBIC**	**w_i**
Nectar-specialists						
1	D * Treatment + D * S + T + FA + W + PF + P	12	-1548.22	3172.46	0.00	0.99
2	D * Treatment * S + T + FA + W + PF + P	14	-1546.19	3181.07	8.60	0.01
3	D * Treatment + S + T + FA + W + PF + P	11	-1572.96	3215.60	43.14	0.00
4	D * Treatment + Treatment * S + T + FA + W + PF + P	12	-1571.64	3219.30	46.83	0.00
5	D * S + Treatment + T + FA + W + PF + P	11	-1617.94	3305.56	133.10	0.00
Nectar-opportunists						
1	D * Treatment + S + T + FA + W + PF + P	12	-1110.64	2297.51	0.00	0.77
2	D * Treatment + Treatment * S + T + FA + W + PF + P	13	-1109.18	2300.95	3.44	0.14
3	D * Treatment + D * S + T + FA + W + PF + P	13	-1110.24	2303.06	5.55	0.05
4	D + S + T + FA + W + PF + P	10	-1120.43	2304.39	6.88	0.03
5	D + T + FA + W + PF + P	9	-1124.11	2305.4	7.89	0.02
Non-nectarivorous						
1	D + S + T + FA + W + PF + P	9	-984.94	2026.06	0.00	0.83
2	D * S + Treatment + T + FA + W + PF + P	11	-980.83	2030.33	4.27	0.10
3	D + Treatment + S + T + FA + W + PF + P	10	-984.93	2032.29	6.24	0.04
4	D * Treatment + D * S + T + FA + W + PF + P	12	-979.13	2033.17	7.11	0.02
5	D * Treatment + S + T + FA + W + PF + P	11	-983.12	2034.9	8.84	0.01

[a] D = Distance of survey plot from garden (0 m, 50 m, 100 m or 150 m); Treatment = feeder or control; S = Season (summer or winter); T = time of day (morning or afternoon); FA = floral abundance in each plot; W = wind speed during survey; PF = previous feeder presence in garden (TRUE or FALSE); P = pet presence on property (TRUE or FALSE)

Nectar-specialists

The model best explaining nectar-specialist abundance included a treatment-distance interaction and a season-distance interaction (Table 1.2: w_i = 99%, R^2m = 0.48, R^2c = 0.88) (see Supplementary Information: Table S1.3 for the full model set & Table S1.5 for detailed statistics). Thus, nectar feeders strongly influenced both the relative abundance of nectar-specialists and their local distribution to distances of at least 150 m in natural vegetation along the suburban edge. Nectar feeders attracted higher densities of birds towards gardens (Figure 1.3: μ = 1.02) than gardens without feeders (μ = 0.31). Feeders also decreased their overall densities in the natural vegetation: the sum of the average bird densities in the three natural vegetation plots (Σμ) were lower for feeder treatments (Σμ = 1.01) than for control treatments (Σμ = 1.15). When feeders were absent, nectar-specialist densities were greater in 50 m vegetation plots and declined into gardens (difference in mean densities (Δμ) = -0.12), suggesting that nectar-specialists generally avoid entering gardens. Despite this, when feeders were present, they attracted more birds than the natural flowers in neighbouring 50 m vegetation plots (Δμ = 0.61).

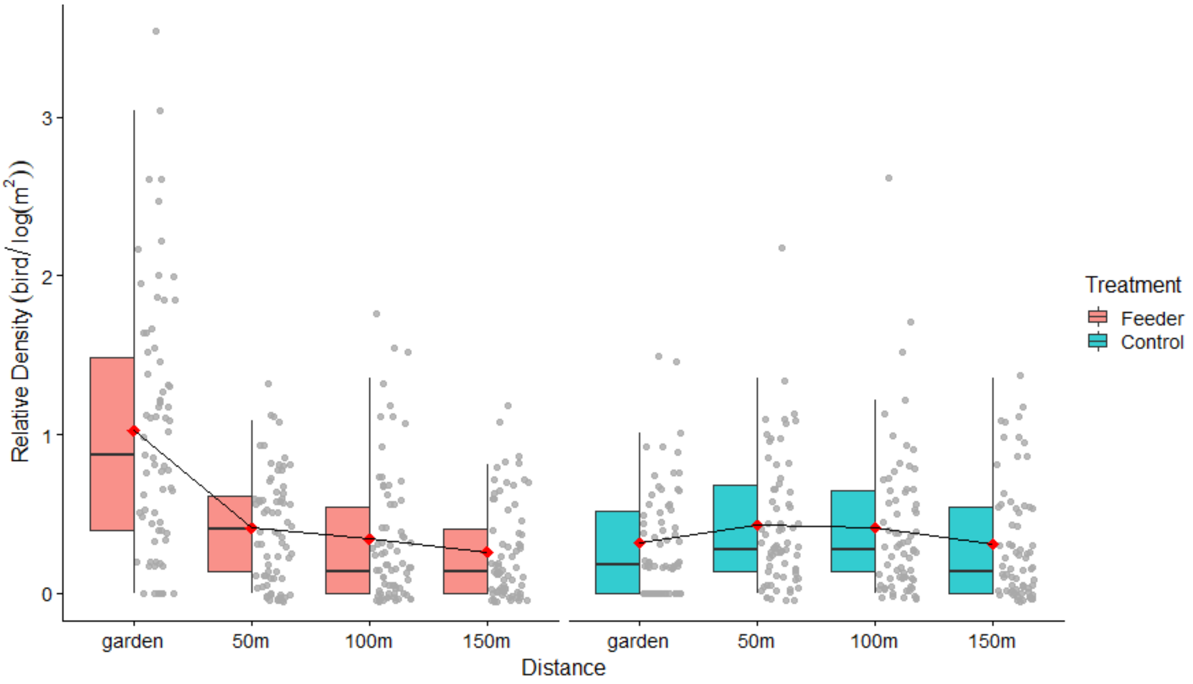

Figure 1.3: Relative densities (bird/log(m^2)) of nectar-specialist birds in gardens and three survey plots in the neighbouring natural vegetation along the urban edge of the Cape Peninsula, for both feeder and control treatments, during winter and summer 2019. Supplementary nectar feeders alter the relative abundance and local distribution of nectar-specialists by attracting more birds towards gardens and decreasing densities of birds in the natural vegetation, whereas gardens without feeders do not. Within each jittered scatterplot, a grey dot represents the total bird density observed during a survey. Box plots show variations in relative bird density and red dots indicate mean bird density (μ) at each survey plot. Grey dots positioned outside the error bars are considered outliers.

The effect of nectar feeders on local nectar-specialist abundance and distribution did not differ with season (Table 1.2) (see Supplementary Information: Table S1.3 for detailed statistics). Thus, feeders attracted more birds to gardens than gardens without feeders, in both summer and winter, despite higher floral abundance in natural vegetation during winter than summer (sum of mean number of flowers/inflorescences in vegetation plots: winter = 4206; summer = 867).

Species-specific responses

As expected, all four nectar-specialist species responded to nectar feeders (Table 1.3). The model including a treatment-distance interaction and a separate species-distance interaction best explained the abundance of the nectar-specialist species (w_i = 98%, R^2m = 0.35, R^2c = 0.72) (see Supplementary Information: Table S1.4 for the full model set & Table S1.6 for detailed statistics). Thus, nectar feeders significantly influenced the relative abundance and local distribution of each of the four species. Not only were higher densities of each species attracted to gardens with feeders than gardens without, but all four species were more abundant in gardens with feeders than in any of the natural vegetation plots (Figure 1.4).

Table 1.3: The top five models to test if the local abundance and distribution of all four nectar-specialist species are affected by supplementary nectar feeders along the suburban edge of the Cape Peninsula. Generalized linear mixed-effect models were constructed, with site as a random factor and the log of size of the survey plots as an offset. For each model, the number of parameters (K), log likelihood (L), Bayesian Information Criterion (BIC), difference in BIC (ΔBIC) from the best model and BIC weight (w_i) is presented. Asterisk (*) indicates both the interaction term and main effect. For each species, 564 observations were made, producing a total sample size of 2256 observations.

Rank	Variables in model [a]	K	L	BIC	ΔBIC	w_i
1	D * Treatment + D * Species + T + FA + W + PF + P + S	17	-2850.94	5833.14	0.00	0.98
2	D * Treatment * Species + T + FA + W + PF + P + S	23	-2831.61	5840.81	7.66	0.02
3	D * Treatment + Species + T + FA + W + PF + P + S	14	-2920.70	5949.50	116.36	0.00
4	D * Species + Treatment + T + FA + W + PF + P + S	16	-2916.45	5956.44	123.29	0.00
5	D * Treatment + Treatment * Species + T + FA + W + PF + P + S	17	-2912.80	5956.86	123.72	0.00

[a] D = Distance of survey plot from garden (0 m, 50 m, 100 m or 150 m); Treatment = feeder or control; Species = species of nectar-specialist bird (Malachite Sunbird, Cape Sugarbird, Orange-breasted Sunbird, or Southern Double-collared Sunbird); T = time of day (morning or afternoon); FA = floral abundance in each plot; W = wind speed during survey; PF = previous feeder presence in garden (TRUE or FALSE); P = pet presence on property (TRUE or FALSE); S = Season (summer or winter)

The significant species-distance interaction demonstrates that the four species followed different distribution patterns along the suburban edge for both feeder and control treatment groups (Table 1.3 & Figure 1.4). Surprisingly, when feeders were absent, Cape Sugarbirds were the most abundant in gardens (Figure 4 D: μ = 0.13), followed by Southern Double-collared Sunbirds (Figure 4 A: μ = 0.10). Densities for Orange-breasted Sunbirds (Figure 1.4 B: μ = 0.04) and Malachite Sunbirds (Figure 1.4 C: μ = 0.04) were equally low in gardens without feeders. When feeders were present, however, Southern Double-collared Sunbird densities were the highest in gardens (μ = 0.31), followed by Cape Sugarbirds (μ = 0.25) and Malachite Sunbirds (μ = 0.25), and lastly Orange-breasted Sunbirds (μ = 0.22).

The extent to which nectar feeders altered their local distributions also differed between species. When feeders were present, Southern Double-collared Sunbird densities followed the steepest increase from 50 m natural vegetation plots into gardens (Figure 1.4: difference in mean densities (Δμ) = 0.23). Moreover, Southern Double-collared Sunbird densities were greater in gardens compared to natural vegetation plots even when feeders were absent, suggesting that they are generally abundant in suburban environments regardless of the presence of feeders. In contrast, there were few Orange-breasted Sunbirds in gardens when feeders were absent, suggesting that, without feeders, they seldom occur in the suburban environment: their densities declined dramatically from 50 m vegetation plots into gardens (Δμ = -0.12). Despite this, nectar feeders were able to attract much greater densities of Orange-breasted Sunbirds to gardens (μ = 0.24) than control gardens (μ = 0.04), even attracting higher densities than any survey plot in the neighbouring natural flora. Similarly, few Malachite Sunbirds visited suburban gardens when feeders were absent, but they also rarely occurred in the natural vegetation plots, at least up to 150 m from the urban edge. Feeders not only increased Malachite Sunbird densities in gardens, but also increased their densities in the 50 m vegetation plots, whereas the overall densities of the other species decreased in the three natural vegetation plots. Thus, while feeders attracted other nectar-specialist species away from the neighbouring natural vegetation, it facilitated Malachite Sunbird presence in the nearby vegetation. This is likely at the cost of attracting them away from deeper interiors of their natural habitat towards the city perimeter. Compared to the other species, changes in Cape Sugarbird densities and distribution patterns in the presence of feeders were less marked, but still detectible.

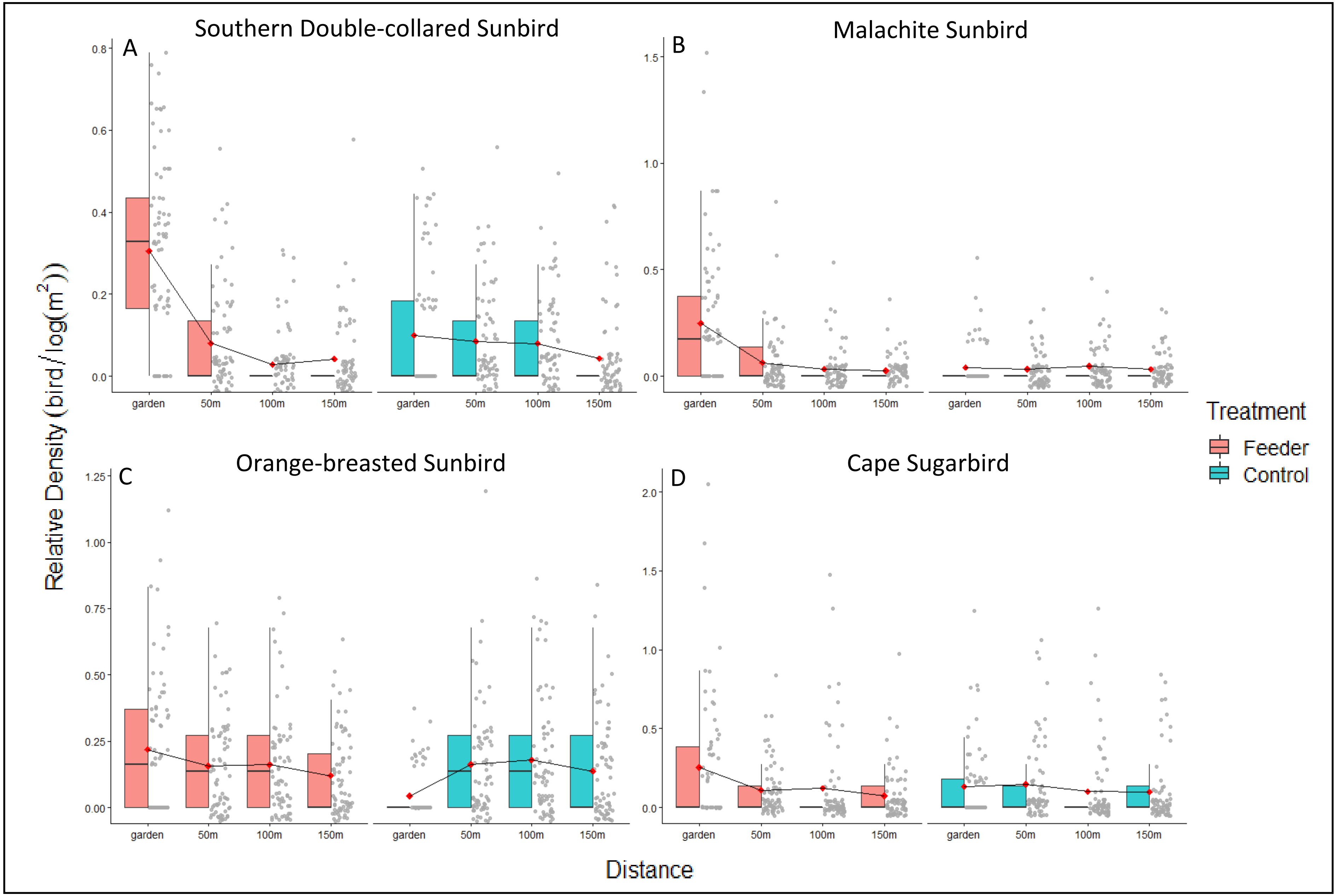

Figure 1.4: Relative densities (bird/log(m^2)) of four nectar-specialist species in gardens and three survey plots in the neighbouring natural vegetation along the urban edge of the Cape Peninsula, for both feeder and control treatments, during winter and summer 2019. Supplementary nectar feeders altered the relative abundance and local distribution of all four species: A) Southern Double-collared Sunbird, B) Orange-breasted Sunbird, C) Malachite Sunbird, and D) Cape Sugarbird. Within each jittered scatter plot, a grey dot represents the total bird density observed during a survey. Box plots show variations in relative bird density and red dots indicate mean bird density (μ) at each survey plot. Grey dots positioned outside the error bars are considered outliers. Note the y-axis scale varies with species.

Nectar-opportunists

For nectar-opportunists, the model including the treatment-distance interaction received the most support (Table 1.2: w_i = 77%, R^2m = 0.67, R^2c = 0.71) (see Supplementary Information: Table S1.3 for the full model set & Table S1.5 for detailed statistics). This result echoes that for nectar-specialists and indicate that nectar feeders affected the relative abundance and local distribution of nectar-opportunistic birds along the suburban edge. Nectar-opportunists appear to be attracted to gardens regardless of the presence of feeders, however (Figure 1.5). This suggests that other factors associated with suburban gardens also attract nectar-opportunistic species. Even so, nectar feeders attracted a much greater density of birds towards gardens (μ = 0.90) than gardens without feeders (μ = 0.46). Feeders also slightly decreased their overall densities in the natural vegetation: the sum of the average bird densities in the three natural vegetation plots (Σμ) were lower for feeder treatments (Σμ = 0.57) than control treatments (Σμ = 0.62).

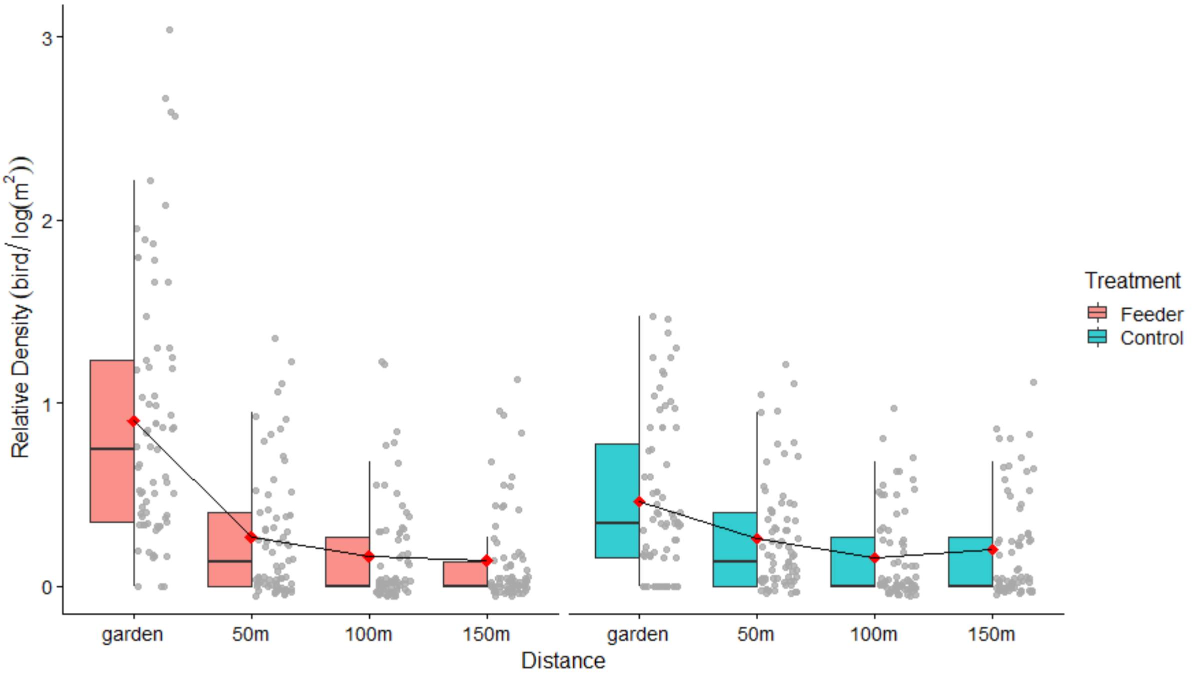

Figure 1.5: Relative densities (bird/log(m^2)) of nectar-opportunistic bird species in gardens and three survey plots in the neighbouring natural vegetation along the urban edge of the Cape Peninsula, for both feeder and control treatments, during winter and summer 2019. Supplementary nectar feeders attracted more nectar-opportunistic birds towards gardens compared to gardens without feeders. Within each jittered scatter plot, a grey dot represents the total bird density observed during a survey. Box plots show variations in relative bird density and red dots indicate mean bird density (μ) at each plot. Grey dots positioned outside the error bars are considered outliers.

The effect of feeders on local nectar-opportunistic bird abundance and distribution did not differ with season (Table 1.2). Thus, nectar feeders attracted more birds to gardens than gardens without feeders in both summer and winter, even though floral abundance in the natural vegetation was higher in winter than in summer (see Supplementary Information: Table S1.5 for detailed statistics).

Non-nectarivores

The model that did not include an effect of feeders best predicted non-nectarivorous bird abundance (Table 1.2: w_i = 83%, R^2m = 0.40, R^2c = 0.77), indicating that nectar feeders had no influence on their local abundance or distribution (see Supplementary Information: Table S1.3 for the full model set & Table S1.5 for detailed statistics). Thus, non-nectarivorous birds were equally abundant in gardens regardless of the presence or absence of feeders and followed similar distribution patterns along the suburban edge of the Cape Peninsula (Figure 1.6). Non-nectarivorous distribution patterns were not affected by season either.

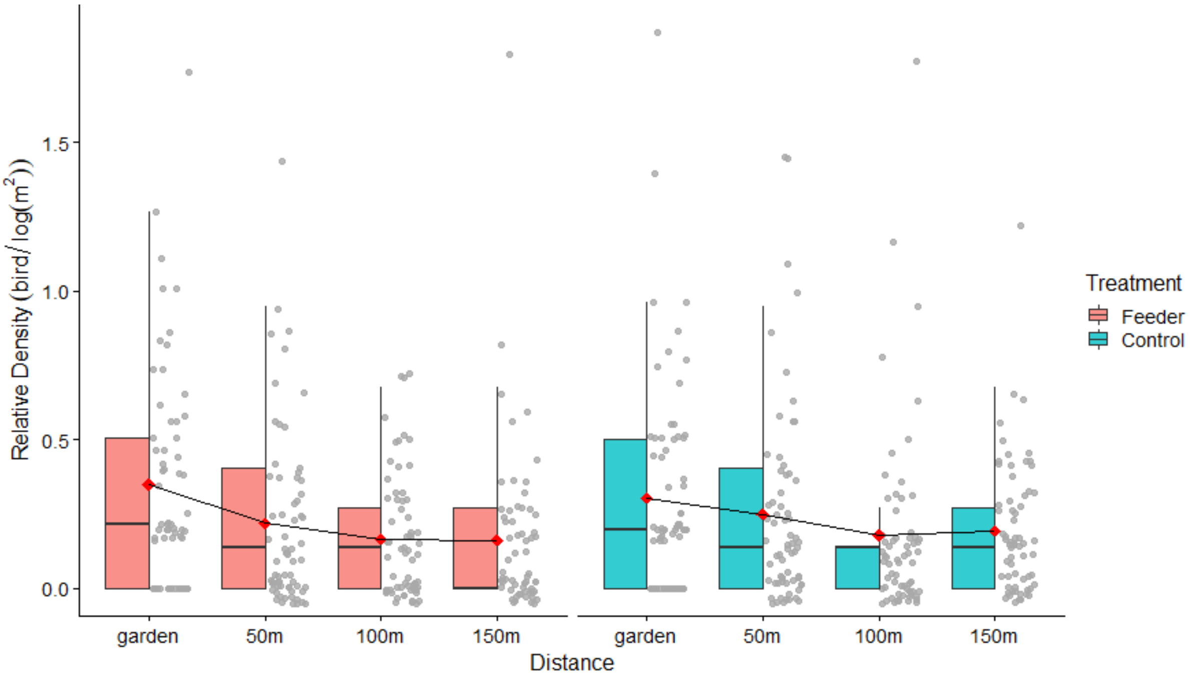

Figure 1.6: Relative densities (bird/log(m^2)) of non-nectarivorous birds in gardens and three survey plots in the neighbouring natural vegetation along the suburban edge of the Cape Peninsula, for both feeder and control treatments, during winter and summer 2019. Supplementary nectar feeders did not influence local non-nectarivorous bird densities or distributions. Within each jittered scatter plot, a grey dot represents the total bird density observed during a survey. Box plots show variations in relative bird density and red dots indicate mean bird density at each plot. Grey dots positioned outside the error bars are considered outliers.

Discussion

This is the first study to experimentally test the effects of supplementary nectar feeders on African bird communities. I set out to test how nectar feeders affect the local abundance and distribution of birds from three feeding guilds (i.e., nectar-specialists, nectar-opportunists and non-nectarivores), and whether these effects differ between wet winter and dry summer seasons. This study is the first to show that nectar feeders in gardens attracted nectarivores over both seasons, even in winter when floral abundance is relatively high in natural vegetation. This finding is particularly important, considering that supplementary feeders also reduced nectarivore abundance in neighbouring natural vegetation. This could suggest that nectarivores may be choosing to visit supplementary feeders over native flowers, even when natural nectar is abundant, which could have implications for their pollination mutualisms. Other results from this study support previous research, however. Consistent with studies on hummingbirds in the Americas (Arizmendi et al. 2007; McCaffrey and Wethington 2008; Avalos et al. 2012; Brockmeyer and Schaefer 2012; Sonne et al. 2016; Greig et al. 2017), I showed that nectar feeders affected both the relative abundance and local distributions of nectar-specialist birds along the suburban edge of the Cape Peninsula. Moreover, like Coetzee et al. (2017 & 2018), I found that nectar feeders increased the densities of both specialist and opportunistic nectarivores in gardens (but not non-nectarivores). The results from this study are unique, however, in finding no seasonal differences in these effects.

Nectar-specialists

Consistent with the findings from Pauw and Louw (2012), the four nectar-specialist species responded differently to the suburban environment when feeders were absent, such that the suburban environment acted as a barrier to some species but not others – this despite that gardens in this study were located only on the urban edge with lower than average housing density, as opposed to gardens from the Pauw and Louw (2012) study that were located in areas with higher housing density. This study further demonstrates that nectar feeders can adjust the sensitivity of specialist nectarivores to the urban landscape by attracting high densities of all four species towards gardens. Nectar feeders also altered their local ranges, although species differed in the extent to which feeders affected their distributions. The similarities and differences between species are discussed below.

Southern Double-collared Sunbirds were abundant in suburban gardens regardless of the presence of feeders, confirming their more generalist status. However, when nectar feeders were present, they attracted even higher Southern Double-collared Sunbird densities to gardens and decreased their densities in the natural vegetation compared to gardens without feeders, suggesting that supplementary nectar feeders have the potential to attract them away from their natural resources.

In contrast to Southern Double-collared Sunbirds, Malachite Sunbirds rarely occurred in gardens and natural areas up to 150 m from the urban edge when feeders were absent, possibly indicating that they are dependent on resources in natural habitat farther away. Given that Malachite Sunbirds have larger nectar requirements than smaller Southern Double-collared Sunbirds, they generally prefer feeding on longer-tubed flowers because they usually contain more nectar (Geerts and Pauw 2009). Such flower types were rare in the gardens and natural areas considered in this study and more abundant higher in the mountains, potentially the reason for their low numbers throughout the surveyed area in the absence of feeders. When feeders were present, however, Malachite Sunbird densities were not only higher in gardens but also in the natural areas close to the edge, compared to when feeders were absent. This could suggest that supplementary feeders drew Malachite Sunbirds in from greater distances, facilitating their presence in gardens and along the suburban perimeter, but likely at the cost of decreasing their densities in natural areas farther away. Future studies would need to conduct surveys deeper into the natural vegetation to determine the range at which feeders may influence sunbird behaviour, especially considering that feeders can attract hummingbirds from as far as 3 km away (Avalos et al. 2012).

Orange-breasted Sunbirds were only in gardens with feeders, confirming that although sensitive to suburban environments (Pauw and Louw, 2012), feeders can overcome their aversion to gardens. Feeders decreased their densities in neighbouring natural vegetation, although less drastically than that of Southern Double-collared Sunbirds. Longer-term exposure to these supplementary food sources could possibly lead to a more conspicuous pattern.

Despite also being considered a “sensitive” species like Orange-breasted Sunbirds (Pauw and Louw 2012), Cape Sugarbirds were the most abundant in gardens when feeders were absent. This may be surprising given that they are the largest of the four nectar-specialist species, and therefore have the highest nectar requirements. However, many gardens in this study contained protea shrubs, which may have affected Cape Sugarbird abundance, considering that this species tightly linked to the distribution of protea resources because proteas contain large amounts of nectar (Geerts et al. 2020). Nevertheless, the presence of nectar feeders further increased Cape Sugarbird densities in gardens, though these changes were not as marked as that of the other species. This is possibly attributable to their highly territorial and competitive behaviour (Calf et al. 2003a) which could limit the maximum number of individuals in a given area, especially around a highly valued and abundant resource such as supplementary feeders.

Contrary to previous findings (Inouye et al. 1991; McCaffrey and Wethington 2008), the effect of nectar feeders on nectar-specialist bird abundance did not differ seasonally. Nectar-specialists were expected to rely less heavily on supplementary feeders and more heavily on natural flower nectar during the wet winter season when floral abundance is higher compared to the dry summer (this study). Instead, nectar-specialists were more abundant at feeders even during winter. Therefore, the strong attraction to nectar feeders seems to break the otherwise strong link between nectarivorous bird density and the temporal distribution of the flowers they feed on. This is potentially concerning if long-term exposure to nectar feeders causes permanent reductions of the nectar-specialist functional group in natural habitat along the city perimeter.

Given that the sugar concentrations in feeders were similar to natural flower nectar (Nicolson and Fleming 2003), these birds may have preferred feeders because they offer a more abundant and more reliable nectar source throughout the year, rather than because they offer better quality food. In fact, natural flower nectar contains minerals and amino acids (Leseigneur et al. 2007) that supplementary sugar water lacks. These quantities are usually small, however, and probably merely supplement the adequate nutrition obtained by feeding on insects (Hainsworth and Wolf 1976; Leseigneur et al. 2007). Thus, feeders are unlikely to provide sub-optimal nutrition to birds, and instead hold a quantity advantage over flower nectar. A recent study (Geerts et al. 2020) shows that nectarivorous bird abundance and diversity is strongly correlated to nectar volume at small spatial scales, providing a probable explanation for their strong attraction to feeders over flower nectar. Birds can spend less time and energy feeding at nectar feeders to satisfy their dietary requirements, although competition and aggression around nectar sources may reduce this advantage. Nectar feeders may therefore provide benefits to birds themselves, but it may come at the expense of decoupling critical bird-pollination networks. Alternatively, it may indirectly benefit the natural vegetation as supplementary feeders draw birds into the area, especially during winter when nectarivores have higher energy demands.

Nectar-opportunists

Opportunistic nectarivores seemed to prefer gardens over specialist natural habitat irrespective of nectar feeder presence. Thus, other features of gardens attract nectar-opportunistic birds. Fynbos vegetation is relatively poor for frugivores, with few plants producing fleshy fruits owing to the nutrient-poor soils (Knight 1988; Fraser 1990), as opposed to suburban gardens with exotic plant species, many of which carry nutritious fruits and seeds or plants that attract insects. These plants probably carry a higher biomass of fruits and seeds compared to natural vegetation, given that people tend to mix fertilizer into the soils and water their plants. Gardens also offer more structure for perching, foraging and nesting than natural vegetation, all of which likely attract generalist birds to gardens. Nonetheless, nectar feeders increased their abundance in gardens and slightly decreased their densities in the natural vegetation. Like nectar-specialists, these effects did not differ between the dry summer and wet winter seasons. Nectar feeders attracted high densities of opportunistic nectarivores to gardens regardless the presence of abundant sources of natural flower nectar in the neighbouring fynbos vegetation, suggesting once again that the attraction of feeders trumped that of flower nectar.

Non-nectarivores

To my knowledge, this is the first study to consider the indirect effects that nectar feeders may have on non-nectarivorous bird species. Non-nectarivores may be negatively affected by the presence of nectar feeders as high concentrations of nectarivores are attracted to gardens, which, in extreme cases, may lead to competitive exclusion. However, the results showed that the local non-nectarivorous bird abundance was not significantly affected by the presence of nectar feeders. This might be expected, because non-nectarivorous birds do not normally feed on nectar sources and would therefore be unlikely attracted to, or benefit from, supplementary nectar sources. It implies, however, that the change in nectarivores' abundance did not have an influence on non-nectarivorous bird abundance either, at least in the short-term. Any long-term effects, e.g., through increased competition for nesting sites or other foraging sources, would need further investigation.

Recommendations

This study demonstrates that even short-term exposure to nectar feeders is enough to significantly alter local nectarivorous bird abundances and distributions. However, longer-term studies are needed to determine whether continuous feeding will permanently reshape bird communities and their distribution ranges (Greig et al. 2017). The ecological effects of nectar feeders would then need further investigation because long-term shifts in pollinator feeding habits could decouple bird-plant pollination interactions (Arizmendi et al. 2007; Avalos et al. 2012). Alternatively, bird numbers may plateau due to intra-specific competition (Tamm 1984) or increased predation risk (Lima 1986; Morosinotto et al. 2017). Future studies should also consider the impact of nectar feeders on bird ranges at a landscape level since feeders may draw birds from considerable distances (Avalos et al. 2012), affecting ecosystems deeper in natural habitat. Telemeters could be used to track changes in bird movement and ranges more accurately. Alternatively, camera traps can be used if birds are colour banded. This could also give insight into the frequency at which individual birds visit nectar feeders.

Prolonged exposure to nectar feeders may have additional consequences for bird communities not considered in this study (e.g., health and reproduction) and would need further investigation. For example, long-term use of feeders may increase disease spread (Bradley and Altizer 2007) as progressively more individuals, from a variety of species, use the same resource. Moreover, nectar feeders may influence breeding success in the long run. A recent study (Coetzee et al. 2020a) demonstrated a higher incidence of breeding sunbirds and sugarbirds in gardens with feeders. This could, in turn, negatively affect non-nectarivorous species as they directly compete with nectarivores for nesting sites and other food sources, though this would need further testing. Future studies could also look at including the effect of different dilutions of sugar-water in different seasons. Nectar-opportunistic birds generally prefer feeding on flowers with lower nectar concentrations than nectar-specialist birds (Brown et al. 2010; Johnson and Nicolson 2008) and may therefore be more attracted to feeders with lower sugar concentrations, especially in summer when they can use it as a water source.

Conclusion

The overall results support the hypothesis that the presence of supplementary nectar feeders influence the relative abundance and small-scale distributions of fynbos nectarivores by attracting higher densities of birds to gardens, relative to the natural vegetation. The attraction of feeders was overall greater than the repelling effect of the suburban environment in both winter and summer, even for “sensitive” (Pauw and Louw 2012) specialist nectarivores, such as Orange-breasted Sunbirds, probably because the feeders offer a relatively abundant food source.

This study provides the first experimental evidence that nectar feeders can facilitate the existence of all four nectar-specialists in Cape Town suburbia, supporting the observational findings of Coetzee et al. (2018). This suggests that nectar feeders can adjust nectarivores’ urban sensitivity, which may be important for their resilience to land-use change. Nectar feeders may thus help to restore the nectar-specialist feeding guild in the suburban environment of Cape Town, currently deprived of its natural pollination processes (Pauw and Louw 2012). While the experiments in this study were only conducted along the urban edge, it provides evidence that nectar feeders have the potential to create stepping-stones to facilitate bird-pollinator movement throughout the city (Pauw and Louw 2012), though this would require further testing. Conversely, however, this study highlights that nectar feeders may have potential negative effects on the surrounding natural ecosystem. Nectar feeders seemingly drew specialist species away from their natural food sources towards suburbia, even when natural nectar was abundant in the fynbos vegetation. In turn, this could affect the pollination processes of local bird-pollinated plant species. It is therefore vital to further investigate the effects that nectar feeders may have on the surrounding environment, particularly natural bird-pollinated plant populations in the Cape Fynbos.

There is clearly much to learn about the effects of supplementary nectar feeding, not only for bird communities but also for the natural ecosystem, and this study provides one of the first steps toward understanding these consequences. This study demonstrates that nectar feeders can significantly affect local nectarivorous bird abundances, at least in the short-term, highlighting the importance to consider the negative and positive consequences before we engage in this popular pastime.

CHAPTER THREE

Do supplementary nectar feeders affect the visitation rate of bird-pollinated Erica *species on the urban edge of the Cape Fynbos, South Africa?*

Abstract

Bird-pollinated plants and their pollinators are highly interdependent. It is therefore vital to identify potential threats to either partner in the mutualism. A rising concern is the indirect effects of supplementary nectar feeders on bird-plant interactions. Nectar feeders provide nectarivorous birds with a relatively abundant alternative food source and could outcompete native flowers for visits by birds, with consequences for their reproduction. Alternatively, increased bird abundance around feeders could facilitate visits to local flowers. This is the first study to investigate the effect of nectar feeders on an African pollinator-plant mutualism. Given the ecological importance of bird pollination in the Cape Floristic Region (CFR), this study was conducted in the Cape Peninsula of Cape Town, South Africa. I carried out a feeding experiment during which nectar feeders were present and absent for seven days in a matched pairs design in gardens on the suburban edge. I tested for the effect of nectar feeders on the floral visitation rate to two bird-pollinated *Erica* species (*Erica plukenetii* subsp. *plukenetii* and *Erica abietina* subsp. *atrorosea*) in the neighbouring vegetation during peak flowering season in winter 2019. Specifically, I compared the change in visitation rate at 10–300 m distances from the gardens before and after the experiment between feeder and control treatment groups. I show that avian pollinators reduced their visitation to *E. plukenetii* flowers, but not to *E. abietina*, in the presence of nectar feeders compared to controls. Nectar feeders in gardens appeared to compete with the local flowers of *E. plukenetii* as far as 300 m from the suburban edge. The neutral effect on *E. abietina* visitation possibly indicates that effects of feeders on ericas are species-specific. This study provides evidence that supplementary feeding can inadvertently interfere with bird-plant pollination networks. This is particularly concerning in the CFR where many bird-pollinated plants species occur near urban areas.

Key words: *artificial nectar feeders, avian nectarivores, bird feeding, bird pollination, indirect effects in human-wildlife interactions, ornithophily, plant-animal interaction, sugar water feeders*

Introduction

Pollinators and the plants they pollinate are highly interdependent (Pauw 2019), so it is vital to identify any potential threats to either of the partners (Cronk and Ojeda 2008). As with most pollination systems, human activities threaten avian pollination across the world (Bond 1994; Kearns et al. 1998; Geerts and Pauw 2011b, b; Pauw and Louw 2012; Şekercioğlu et al. 2016). Supplementary bird feeding is a popular recreational activity, yet its ecological effects have been rarely studied (Reynolds et al. 2017). A concern is the indirect effect of supplementary nectar feeders on bird-plant pollination mutualisms, because nectar feeders significantly affect the abundance and distribution of nectarivorous birds (Chapter 2), and therefore likely alter bird visitation to nearby flowering plants. To date, only a few studies have considered its effect on pollination networks and have had conflicting results (Arizmendi et al. 2007; McCaffrey and Wethington 2008; Avalos et al. 2012; Brockmeyer and Schaefer 2012; Sonne et al. 2016; Maguina and Muchhala 2017). It remains unclear whether increased nectarivorous bird abundance owing to nectar feeder presence translates into increased visitation to local flowers, or whether feeders outcompete native flowers for bird attention. This uncertainty is unsettling given that the provisioning of supplementary nectar is a common garden activity (Coetzee et al. 2020a).

Urbanization causes fragmentation of the landscape and changes the distribution of nectar sources by replacing floral resources in the natural vegetation with exotic garden plants and bird feeders (French et al. 2005). Human-dominated areas reduce the functional diversity of the nectarivore guild by limiting the movement of urban-sensitive nectarivorous bird species (Pauw and Louw 2012). Consequently, some plants in natural fragments suffer low reproductive rates (Geerts and Pauw 2009, 2012; Geerts 2016). However, when nectar supply becomes scarce in natural vegetation, some avian pollinators can cross urban areas to track native flowering species in remnant fragments, or even adapt to the urban landscape by expanding their diet to non-native flowering plants and supplementary food sources (Inouye et al. 1991; Geerts and Pauw 2009; Neuschulz et al. 2013). It has been suggested that nectar feeders can be used to facilitate the crossing of nectarivorous birds into the urban landscape and act as stepping stones between habitat fragments (Pauw and Louw 2012; Coetzee et al. 2018). Nectarivorous bird abundance is tightly linked to the distribution of nectar resources at small spatial scales (Geerts et al. 2020); consequently, nectar feeders can attract high densities of nectarivorous birds (Chapter 2) (Inouye et al. 1991; Arizmendi et al. 2007; McCaffrey and Wethington 2008; Avalos et al. 2012; Brockmeyer and Schaefer 2012; Sonne et al. 2016) since they offer a super-abundant resource of similar nutritional quality to flower nectar (Nicolson 2007). This attraction is stronger than the aversion of the suburban environment even for otherwise urban-sensitive bird species (Chapter 2). However, given that nectar feeders can significantly influence nectarivorous bird abundance and distribution (Chapter 2), they likely also affect birds' natural foraging behaviour (Arizmendi et al. 2007; McCaffrey and Wethington 2008; Avalos et al. 2012).

Whether the effects of nectar feeders are negative or positive is not well understood, however. There is some evidence from hummingbird systems that provisioning large quantities of supplementary sugar-water decreases bird visitation to local nectar-producing flowers, with consequences for their reproductive success (Arizmendi et al. 2007; McCaffrey and Wethington 2008; Avalos et al. 2012). Insufficient pollen loads due to reduced visitation rates to flowers can cause declines in plant fecundity, potentially decreasing population size, and causing changes in plant species composition towards, for example, wind-pollinated plant species (Aguilar et al. 2006; Mortensen et al. 2008; Anderson et al. 2011; Geerts and Pauw 2012; Thomann et al. 2013; Regan et al. 2015; Geerts 2016). In contrast, however, there is also evidence of increased visitation to flowering plants close to nectar feeders as avian pollinators are drawn into the area (Brockmeyer and Schaefer 2012; Sonne et al. 2016). Moreover, previous work has only been conducted on hummingbird and bat pollination systems in the Americas and remains to be tested in other bird-plant systems elsewhere in the world.

A better understanding of the effects of nectar feeders on African pollination systems is especially important because land-use changes in many developing countries are already affecting bird-plant interactions. In the Cape Floristic Region (CFR), a biodiversity hotspot in the southwestern tip of South Africa (Myers et al. 2000), bird-plant interactions are threatened by the interacting effects of habitat fragmentation, urbanization, road traffic, alien plant invasion, disturbed fire regimes and honeybee farming (Fraser and Crowe 1990; Rebelo 1992; Geerts and Pauw 2011a, b; Geerts et al. 2012; Pauw and Louw 2012; Lee and Barnard 2016). Moreover, birds are key to the maintenance of a disproportionately large percentage of plant species in the fynbos biome of the CFR. The bird-pollinator to plant species ratio is unusually high, with over 300 plant species relying on only six nectar-specialist bird species for their pollination (Rebelo 1987). Only four of these bird species occur throughout the biome. Two are endemic to it, Cape Sugarbird (*Promerops cafer*) and Orange-breasted Sunbird (*Anthobaphes violacea*), and two are more widespread, Southern Double-collared Sunbird (*Cinnyris chalybeus*) and Malachite Sunbird (*Nectarinia famosa*). Despite this system being asymmetrical, the interaction between these birds and the plants they pollinate are relatively specialized and comparable to that of hummingbird–plant communities (Feinsinger 1978; Brown and Bowers 1985; Bond 1994; Hockey et al. 2005; Geerts and Pauw 2009; Zanata et al. 2017). Plant species with specialized pollination systems are particularly vulnerable to population decline (Bond 1994) when their pollinators declines.

An example of a specialized pollination system in the CFR is the *Erica*-sunbird mutualism. The genus *Erica* (Ericaceae) is typically a prominent element in fynbos vegetation and is the largest genus of the CFR (Oliver et al. 1983; Oliver and Forshaw 2012). Approximately 15% of the 680 *Erica* species in the CFR are potentially bird pollinated, and provide one of the main nectar sources for the endemic Orange-breasted Sunbird, the main pollinator of these ericas (Rebelo et al. 1984, 1985; Geerts and Pauw 2009). Although this sunbird is usually uncommon in urban gardens, it makes considerable use of nectar feeders in areas such as the Cape Peninsula on the edges between natural habitat and suburbia (Coetzee et al. 2018). This affects the abundance and distribution of these birds (Chapter 2) and is likely to also affect their patterns of floral visitation. Increased garden visitation could thus influence pollination success, affecting *Erica* populations on the suburban edge. Such processes could exacerbate the effects of ongoing habitat degradation which has already transformed large parts of the former *Erica* distribution range in the Cape, threatening more than 180 *Erica* species, particularly in lower lying areas (Rebelo 1992). Many of the remaining populations occur in small and isolated fragments across the City of Cape Town (Rouget et al. 2003). Moreover, most bird-pollinated *Erica* species in the southwestern Cape are self-sterile and dependent on pollinators for their reproductive success (Arendse 2015; Angoh et al. 2017; Coetzee et al. 2020b), which makes them especially vulnerable to further deterioration of ecological interactions.

Here, I investigated the indirect effect of supplementary nectar feeders on an African bird-plant system during peak flowering season. I carried out a field experiment along the suburban edge of the Cape Peninsula to test whether nectar feeders in gardens influence the visitation rate to *Erica plukenetii* and *E. abietina* in the neighbouring fynbos vegetation. I asked whether avian pollinator visitation rates (1) differ between plants near gardens with supplementary nectar feeders and near control gardens without feeders, and (2) vary with distance from each type of garden. Nectarivorous birds are likely satiated by the enormous amounts of supplementary nectar and therefore, I expected to see lower visitation rates to *Erica* plants near gardens with feeders, compared to plants near gardens without feeders. I also expected *Erica* flowers closer to garden edges to receive fewer pollinator visits relative to flowers further away.

Methods

Study area

Research was conducted in the suburbs of the southern Cape Peninsula, South Arica. This study area falls within the species-rich Cape Floristic Region (CFR), a biodiversity hotspot home to many endemic plant species (Linder 2005; Holmes et al. 2012) and where bird pollination plays a key ecological role (Rebelo et al. 1984). Study sites comprised 17 gardens on the suburban edge of Scarborough, Simon's Town, Glencairn and Clovelly (Figure 1.1), along with their bordering natural vegetation extending approximately 300 m from the fire break (~10 m wide) which divides the urban edge from natural vegetation. The suburban edge was chosen as the focus study area because plant populations in natural habitat closest to residential areas likely experience the strongest effects from nectar feeders.

Study species

I obtained visitation rate data for two co-flowering *Erica* species (*Erica plukenetii* subsp. *plukenetii* and *Erica abietina* subsp. *atrorosea*) on the suburban edge during their peak flowering season in winter (May and June) 2019 (Figure 2.1). Both species grow to 1 m in height, and are woody shrubs found on rocky or sandy mountain slopes. They produce clusters of flowers with long, tubular corollas, indicating pollination by birds (Rebelo et al. 1985). Both species are colour polymorphic, but both had dark pink flowers at the study sites. *Erica abietina* subsp. *atrorosea* is endemic to the Cape Peninsula and flowers from midsummer to early spring (December to August). *Erica plukenetii* is a common species in montane fynbos found throughout the western part of the CFR (Goldblatt and Manning 2000). Flowering time for *E. plukenetii* varies spatially but it flowers predominantly in winter in the Cape Peninsula (March to September).

Figure 2.1: Visitation rate was monitored for two *Erica* (Ericaceae) species common along the suburban edge of the Cape Peninsula, namely A) *Erica abietina* subsp. *atrorosea* and B) *Erica plukenetii* subsp. *plukenetii*.

Visitation rate experiments

Gardens were selected following the criterion that healthy, mature *Erica* shrubs were present in the fynbos vegetation within roughly 200 m of the property. To ensure independence of visiting birds, gardens were at least 250 m apart. One to six *Erica* plants (depending on their abundance) were selected in each of two to six patches of approximately 10 x 10 m (100 m^2), at each site, at varying distances from the edge of the fire break (Figure 2.2).

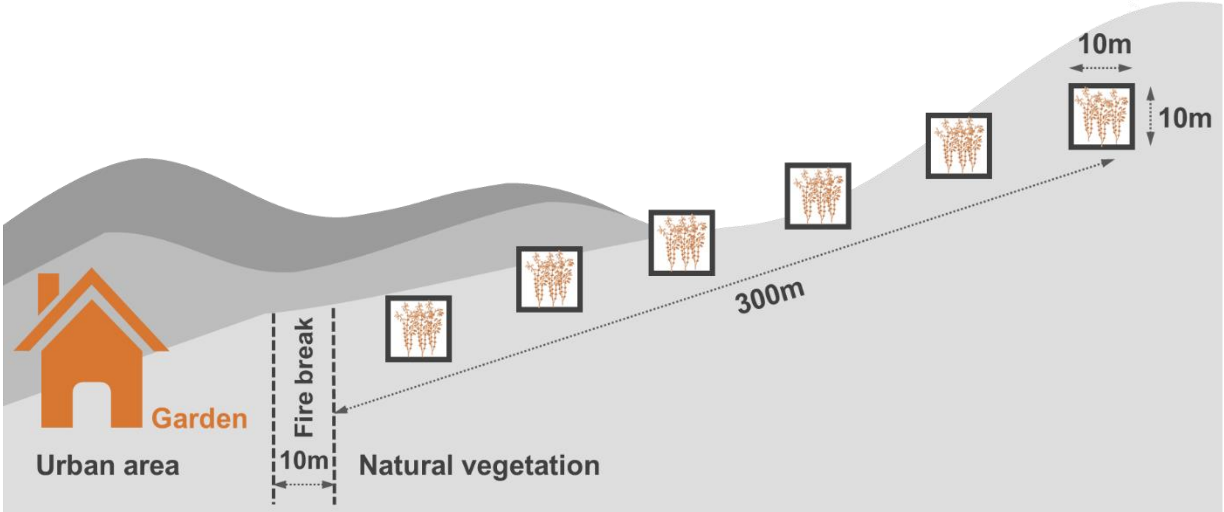

Figure 2.2: A summary diagram of the experimental design at the 17 sites in this study, for both control (n = 7) and treatment (n = 10) groups. Squares indicate patches (10 x 10 m) containing *Erica* plants (unit of analysis) at a range of distances from the urban edge (up to 300 m).

To investigate the effect of nectar feeders on *Erica* pollinator visitation rate, I conducted a seven-day feeding experiment in which nectar feeders were experimentally present and absent in a matched pairs design. I randomly divided the 17 sites into experimental and control treatments so that nectar feeders were placed in 10 gardens and the remaining 7 gardens had no feeders. Feeder treatments consisted of four feeders placed in clusters in the gardens to provide a concentrated source of nectar to increase detection by birds and mimics the bird-feeding habits of many garden owners. Feeders were frequently refilled to maintain a continuous supply of sugar water throughout the seven-day experiment. The sucrose solution was equivalent to the average concentration in the specialist nectar of southern African bird-pollinated plants (20% weight/weight) (Nicolson and Fleming 2003).

Given that direct observation of pollinator visitation is time consuming, Geerts and Pauw (2011a) demonstrated that the anther ring status of *Erica* flowers provides an easily quantifiable proxy for their visitation rates by sunbirds. Before a visit, *Erica* anthers are fused into a ring (Figure 2.3 A). When sunbirds visit these flowers, their probing beaks rupture the anther rings and pollen is released (Figure 2.3 B) (Rebelo et al. 1985; Schumann et al. 1992). Using this method, I quantified the proportion of total flowers visited for each *Erica* plant twice: (1) before nectar feeders were placed in gardens and (2) after feeders were stationed in the gardens for seven days. Note that this method only demonstrates whether a flower was visited at least once and therefore does not give information on the number of times the flower was visited. Since nectar resource abundance is known to affect per-plant visitation rates (Schmid et al. 2015, 2016; Nottebrock et al. 2017; Geerts et al. 2020), I estimated floral abundance in each patch as the total number of healthy, mature flowers of any bird-pollinated species, not just the two focal *Erica* species in this study, or inflorescences (e.g., bird-pollinated *Protea* species). Avian nectarivores sometimes visit open mouthed *Erica* species which are extensively visited by insects (Rebelo et al. 1985), but these were not abundant in my study site and were therefore not accounted for in this study.

Statistical analyses

All data exploration and analyses were conducted in R 3.6.1 (R Core Team 2019) and considered the two *Erica* species separately. I evaluated models for deviations from assumptions by plotting the normalized residuals against the fitted values and inspecting histograms of the normalized residuals. Multi-collinearity assessments using Variance Inflation Factors (VIFs) showed that none of the predictor variables had strong relationships (VIFs < 3).

The response variable for each *Erica* species was calculated in two steps. First, I calculated the proportion of flowers visited for each plant before and after the seven-day feeding experiment separately. Next, I subtracted the proportion of flowers visited after the experiment from the proportion visited before to determine the change in visitation rate to *Erica* flowers. Negative values were produced when some flowers on a plant died or new flowers bloomed during the seven days, such that the proportion visited before the experiment was greater than after.

The main goal in this study was to test whether different treatments (feeder vs. control) resulted in different visitation rates to *Erica* flowers and whether this effect differed with distance from the feeders. This predicts a significant interaction between treatment type and distance. To test this, I fitted linear mixed-effects models for each species separately using the lmer function from the lme4 package (Bates et al. 2015). The full statistical models are of the form:

$$\begin{aligned}&Change\ in\ visitation\ rate \sim Distance * Treatment + (1|Site),\\&\qquad weights\ =\ sqrt\ (Total\ number\ of\ flowers)\end{aligned}$$

where * indicates an interaction between *treatment* (categorical with two levels) and *distance* (continuous). Floral abundance in each patch and the presence of previous feeders in gardens did not significantly predict *Erica* visitation rate in the full model and so were dropped from the final model. Site was modelled as a random intercept effect to account for multiple sampling plants per site. Patch ID was not included as a random factor in the final models because the proportion of variance explained was zero. I included a weights term in the models as the square root of the number of flowers on each plant, giving slightly more weight to plants with more flowers as these provided a more robust estimate of visitation rate. Number of flowers was taken as the mean of the total number of flowers before and after the experiment.

To compare treatment groups and determine the magnitude of the effect on visitation rate, I calculated effect sizes as the difference between means (Δµ) with 95% confidence intervals (provided in square brackets with Δµ) using the emmeans package (Lenth 2020). If a confidence interval did not include zero, the difference between the treatment groups was considered statistically meaningful, and *vice versa*. Additionally, forest-plots of the standardized estimates were produced using the sjPlot package (type = std) (Lüdecke 2020) and is provided in the supplementary material (Figure S2.1). To assess the goodness-of-fit for the models, I used the r.squaredGLMM function in the MuMIn package (Barton 2012) to calculate the marginal (R^2m) and conditional pseudo-R^2 values (R^2c), which indicate the variation in the data explained by fixed effects, and by both fixed and random effects, respectively (Nakagawa and Schielzeth 2013).

Results

All four nectar-specialist bird species (*Anthobaphes violacea, Promerops cafer, Nectarinia famosa* and *Cinnyris chalybea*) visited supplementary nectar feeders within at least four days across the study sites (Chapter 2). Before feeding experiments, avian pollinators visited on average a larger proportion of flowers from *E. abietina* plants compared to *E. plukenetii* plants (Δµ = 0.12 [0.05; 0.19]) across all sites, suggesting a pollinator preference towards *E. abietina* flowers under normal conditions. Specifically, before feeders were placed in treatment gardens, birds visited on average 63% of *E. abietina* flowers at control sites and 65% at treatment sites (mean±SD of proportion of flowers visited before experiments: control = 0.63 ± 0.31, treatment = 0.65 ± 0.22), whereas birds visited 49% of *E. plukenetii* flowers at control sites and 56% at treatment sites (control = 0.49 ± 0.23, treatment = 0.56 ± 0.19). After the seven-day feeding experiment, birds visited on average 85% of *E. abietina* flowers at sites with control gardens and 91% at sites with feeders in gardens (mean±SD of proportion of flowers visited after experiments: control = 0.85 ± 0.21, treatment = 0.91 ± 0.18), whereas birds visited 66% of *E. plukenetii* flowers at sites without feeders and 64% at sites with feeders (control = 0.66 ± 0.25, treatment = 0.64 ± 0.23).

Analyses of change in visitation rate showed that supplementary nectar feeders in gardens influenced pollinator visits to at least one of the two *Erica* species in this study (Table 2.1 & Figure

2.4). The linear mixed-effect model indicates that, on average, birds visited 16% fewer *E. plukenetii* flowers at feeder versus control sites during the seven-day experiment (Δμ = -0.16 [-0.31; -0.01], R^2m = 0.01, R^2c = 0.02). The distance-treatment interaction was not significant, however, suggesting that feeders had a similar effect on *E. plukenetii* visitation at all distances up to 300 m. There was a trend for higher visitation to *E. abietina* flowers in the presence of feeders than without, but this effect was not statistically significant (Δμ = 0.21 [-0.35; 0.77], R^2m = 0.04, R^2c = 0.12). The confidence intervals are wide, however, indicating a high level of uncertainty which could be attributable to the relatively small sample size for *E. abietina* (n = 69 plants) because sampling was conducted towards the end of its flowering period, compared to the more abundant, peak-flowering *E. plukenetii* (n = 153 plants).

Table 2.1: Results from the linear mixed-effects models for *Erica plukenetii* (*n* = 153 plants) and *Erica abietina* (*n* = 69 plants) to determine whether supplementary nectar feeders affect visitation rate along the suburban edge of the Cape Peninsula. Site was included as a random factor. The parameter estimates, lower limits (LL) and upper limits (UL) of the 95% confidence intervals (CI), standard error (SE), degrees of freedom (df), t-values and *p*-values for each variable are provided here. Significant *p*-values are highlighted in bold.

			95% CI				
Variable	**Estimate**	**LL**	**UL**	**SE**	**df**	**t**	***P***
E. plukenetii							
Intercept	0.188	0.188	0.192	0.03	17.23	5.45	**0.000**
Distance	-0.018	-0.018	-0.016	0.03	111.44	-0.69	0.493
Treatment (Feeder)	-0.107	-0.107	-0.104	0.05	20.14	-2.18	**0.041**
Distance : Treatment (Feeder)	0.054	0.054	0.058	0.05	142.02	1.17	0.243
E. abietina							
Intercept	0.138	0.134	0.175	0.10	7.75	1.40	0.200
Distance	0.110	0.109	0.117	0.07	33.01	1.65	0.108
Treatment (Feeder)	0.136	0.133	0.175	0.14	7.39	1.00	0.349
Distance : Treatment (Feeder)	0.000	-0.001	0.013	0.09	45.14	0.00	0.998

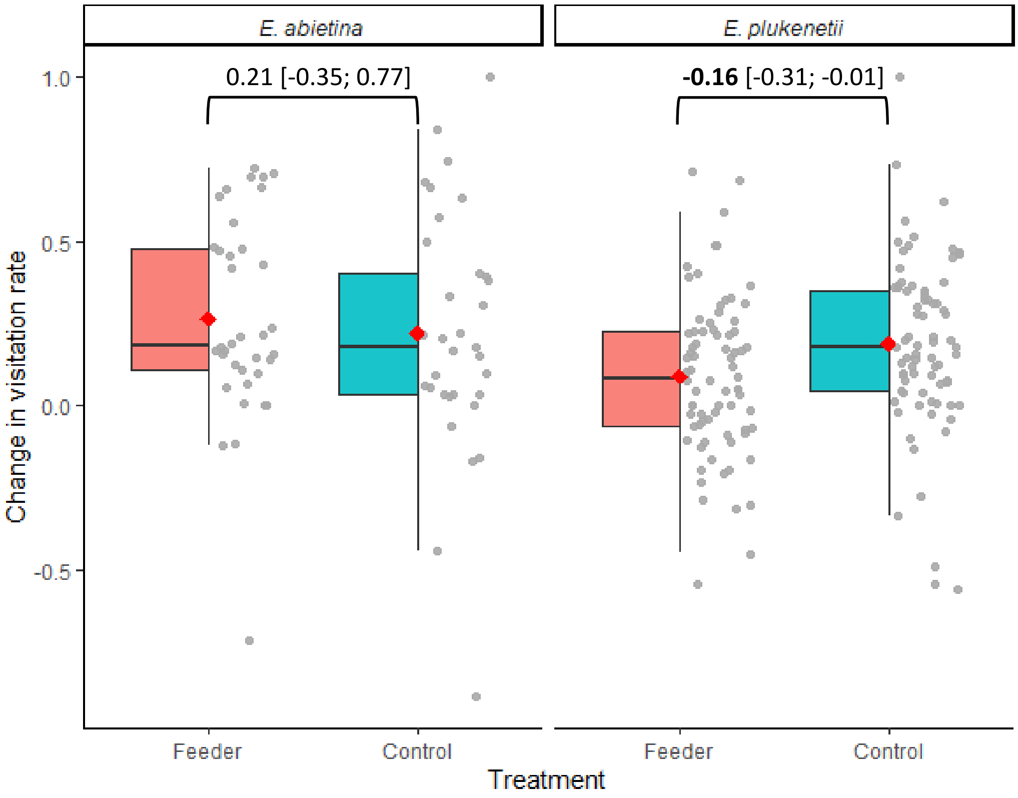

Figure 2.4: Change in visitation rate of *Erica plukenetii* and *E. abietina* flowers after a seven-day feeding experiment along the suburban edge of the Cape Peninsula for both feeder and control treatments. Supplementary nectar feeders only significantly decreased *E. plukenetii* visitation. A grey dot represents the difference between the proportion of flowers visited on an individual plant before and after the feeding experiment. Grey dots positioned outside the error bars are considered outliers. Red diamonds indicate mean change in visitation rate. The unstandardized effect size is given as the difference between means of the treatment groups with 95% confidence intervals (provided in square brackets).

Discussion

This is the first study to consider the effect of supplementary nectar feeders on an African bird-pollination system. I experimentally tested whether nectar feeders in gardens on the suburban edge affect the visitation rate of two bird-pollinated *Erica* species in the neighbouring fynbos vegetation. Experimental addition of nectar feeders negatively influenced bird visitation to one *Erica* species (*E. plukenetii*) but not the other (*E. abietina*), suggesting that the magnitude of the effect of feeders on ericas is species specific. The effect of feeders on specialist nectarivore visitation rate to *Erica plukenetii* did not vary with distance from feeders and was still detectable at 300 m from the feeders. Future experiments stretching deeper into the vegetation are necessary to reveal whether effects of nectar feeders on pollination services extend beyond the 300 m range considered in this study.

This result is consistent with my behavioural observations in Chapter 2 in which I demonstrated that feeders drew nectar-specialist birds away from natural vegetation towards gardens. If birds spend more time around feeders and less time in natural vegetation, it is sensible to expect lower visitation rates to local flowers. This finding is also consistent with two previous studies on hummingbirds (Arizmendi et al. 2007; Avalos et al. 2012), but contrasts with other studies which demonstrated neutral or positive effects of bird feeders on plant reproductive fitness (Brockmeyer and Schaefer 2012; Sonne et al. 2016). These opposing results could in part be explained by the amount of time the feeders were available to birds. Feeders were present for short-term periods in this study (7 days) and that of Arizmendi at al. (2007) (1 day), but present for several years in the case of the other studies (Brockmeyer and Schaefer 2012; Sonne et al. 2016). Long-term exposure to nectar feeders could provide enough time for nectarivorous birds to form dominance hierarchies around feeders and adjust demographically to feeder presence. As competition increases and dominant individuals monopolize the feeders, subordinate individuals may find the surrounding flowers increasingly attractive, eventually neutralizing the initial negative effect. Yet, Avalos et al. (2012) found that permanent feeder presence continues to negatively influence the pollination processes of hummingbird-pollinated species in Costa Rica, contrary to this hypothesis.

Although visitation rate gives valid information about the pollination services provided by nectarivorous birds, it is not a direct measure of plant reproductive fitness and actual pollen deposition would have given more robust results when assessing pollination rate. Future work would also need to address whether reduced visitation to *E. plukenetii* flowers as a result of feeder presence translates into reduced seed set. This is a reasonable assumption, however, considering that the ecotype of *E. plukenetii* in our study area relies almost exclusively on avian pollinators for successful pollination (Van der Niet et el. 2014; Arendse 2015; Angoh et al. 2017; Coetzee et al. 2020b), and that exclusion experiments have shown a reduction in the seed set of *E. plukenetii* in the absence of Orange-breasted Sunbirds (Botha 2017).

The two *Erica* species were influenced in different ways by nectar feeders. When offered supplementary food, avian pollinators reduced their visits to *E. plukenetii* flowers but did not detectably change their visitation to *E. abietina* flowers. It is possible that the high uncertainty, attributable to the small *E. abietina* sample size, masks the true effect of feeders on its visitation. Alternatively, the absence of an effect of feeders may be real, supporting Brockmeyer and Schaefer (2012) who found that the effect of feeders was species-specific: while feeders had no effect on most plant species in their taxonomically diverse dataset, other species received fewer or increased visits close to feeders. It seems that sunbirds tend to prefer *E. abietina* over *E. plukenetii* under normal conditions and this preference could be amplified in the presence of an alternative food source because it influences the relative profitability of the less-preferred species. Differences in nectar properties could provide insight into possible preferences because other sunbird species have been found to prefer flowers with larger nectar volumes and higher sugar concentrations (Nicolson and Fleming 2003; Brown et al. 2010). The average nectar volume in flowers of *E. abietina* is less than that of *E. plukenetii* (see Supplementary Material: Figure S2.3), making nectar volume an unlikely explanation. Nectar sugar content could be a more plausible explanation because nectar in *E. abietina* flowers is more concentrated than in *E. plukenetii* (see Supplementary Material: Figure S2.2). Other potential drivers of sunbird preference may include differences in inflorescence architecture or floral display size (*E. plukenetii*: mean 133 flowers/plant vs. *E. abietina*: mean 54 flowers/plant) between species. Nevertheless, the exact factors influencing any species-specific effect of feeders awaits further investigation. Moreover, it is possible that the effects of nectar feeders on flower visitation may be more marked in dry summer when flowers are scarce, because sunbirds may choose to primarily visit feeders and ignore the few remaining flowers (Inouye et al. 1991; McCaffrey and Wethington 2008).

Other plant families not considered in this study may also be affected by nectar feeders. For example, many members from the Proteaceae family rely primarily on the long-billed Cape Sugarbird for their pollination (Skead 1967; Mostert et al. 1980; Collins 1983; Rebelo et al. 1984, 1985; Fraser and McMahon 1992; Geerts and Pauw 2009; Pauw and Johnson 2017), whereas the Malachite Sunbird is the exclusive pollinator of many members from the Iridaceae and Amaryllidaceae families (Geerts and Pauw 2009). Thus, it is necessary for future studies to consider the effect of nectar feeders on a range of plant species from different plant families, including those that are hyper-specialized for pollination by longer-billed avian pollinators.

Conclusion

I conclude that supplying supplementary nectar in gardens on the suburban edge of the Cape Peninsula has the potential to disrupt the pollinator visitation rates of at least some bird-pollinated species. Studies from a wider range of plant species and urban-nature contexts are needed to assess the generality of these effects, particularly for vulnerable plant species with very specialised pollination systems. Despite the remaining uncertainties regarding supplementary feeding, this study highlights the importance of considering the unintended cascading effects of supplementary feeding on the surrounding environment. Seemingly inconsequential human activities like attracting birds to gardens with feeders may not threaten entire populations but could exacerbate existing anthropogenic pressures on pollination systems at city edges. This may be of particular concern in biomes such as the Cape Floristic Region where many endangered endemics and rare plants occur in close proximity to urban areas and numerous plants potentially depend on birds for their reproductive success.

CHAPTER FOUR: Conclusions and Recommendations

Wild bird feeding is a multi-billion-dollar global industry (Jones and Reynolds 2008). Over the years, the practice of bird feeding in residential gardens has changed substantially and currently targets a much broader bird community than merely seed-eating birds (Jones and Reynolds 2008; Plummer et al. 2019). Providing supplementary nectar feeders for nectarivorous birds is a popular garden activity, but how these relatively novel urban sources influence bird abundance patterns is not well understood (Avalos et al. 2012; Greig et al. 2017). Moreover, the ecological impacts of nectar feeders, whether negative or positive, remain largely unknown (Arizmendi et al. 2007; McCaffrey and Wethington 2008; Brockmeyer and Schaefer 2012; Sonne et al. 2016). This lack of information adds to the disparity in opinion among proponents and opponents, and therefore the use of nectar feeders remains heavily debated.

The main aim of this dissertation was to test whether supplementary nectar feeders change bird distributions at a local scale, and in so doing, affect bird-plant mutualisms in the Cape Fynbos. To answer this, the dissertation was divided into two data chapters (Chapter 2 & 3), each addressing the effect of feeders on a specific side of the mutualism. In chapter 2 I focussed on the effect of nectar feeders in suburban gardens on local bird abundance and distribution patterns. In chapter 3 I investigated whether nectar feeders alter avian pollinator visitation rates to bird-pollinated *Erica* species in the neighbouring vegetation.

In Chapter 2, I found that the attraction of nectar feeders was overall stronger than the aversion to the urban environment for nectarivorous birds, and that feeders can facilitate the crossing of urban-sensitive nectarivores into suburbia. This may, at first, appear to be a positive effect by increasing the capacity of urban areas to support avian pollinators and by acting as stepping stones between natural habitat fragments. However, nectar feeders altered the local distributions of nectarivores in both the wet winter and dry summer, drawing them away from natural vegetation into gardens. This suggests that they prefer the superabundant supplementary food source over flower nectar, even when floral abundance is high in neighbouring vegetation. This is particularly concerning in the light of the results from Chapter 3, which indicate that sunbirds decrease their visits to at least *Erica plukenetii* flowers in the presence of nectar feeders. Therefore, supplementary feeding can disrupt pollinator visitation rate to some bird-pollinated species, regardless the floral abundance in neighbouring vegetation. Self-incompatible plant species with specialized pollination systems, such as *E. plukenetii*, would be expected to be vulnerable to the negative effects of feeders because reduced flower visits likely translate into pollinator-limited seed set. Thus, nectar feeders may affect local populations of some bird-pollinated plant species on city edges.

Although *E. plukenetii* received reduced visits in the presence of feeders, no effect of feeders was detected on *E. abietina* visitation rate, suggesting either that effects differ among plant species, or that a real but weaker effect on *E. abietina* was not detected with a smaller sample size for this species. Fully understanding the consequences of nectar feeders for bird-pollinated species will require investigations into more bird-pollinated *Erica* species in different urban-nature contexts. Notably, it is also necessary to consider the effect of nectar feeders on bird-pollinated plant species from a wider variety of plant families, to determine which species are likely to suffer from competition by nectar feeders for bird attention. All four nectar-specialist bird species in this study, including the longer-billed Malachite Sunbird and Cape sugarbird, responded to nectar feeders, and thus plants reliant on them (e.g., Proteaceae and Amaryllidaceae) might also be affected. It would also be useful to determine which traits of plant species make them vulnerable to negative impacts by the presence of nectar feeders. Construction of pollinator networks (e.g., Memmott 1999; Simba et al. 2018) would allow identification of how plant and bird networks are affected by the presence of nectar feeders, and which species are most impacted.

Many uncertainties regarding supplementary feeding remain, but the results from this dissertation reminds us that we need to consider the unintended ecological effects of such seemingly trivial activities. Bird feeding may be a well-intentioned human pastime but increasing the prevalence of supplementary food sources in urban areas could exacerbate the existing pressures on pollination systems in a sensitive biodiversity hotspot. Without further knowledge on the extent to which the ecological consequences of nectar feeders may stretch, it is wiser to adopt precautionary measures. If we aim to restore the nectarivore functional guild to cities, my recommendation is that conservationists rather develop bird friendly gardens using appropriate nectar producing plants to act as stepping stones connecting habitat fragments. Quantitatively comparing the effects of supplementary nectar feeders and bird-friendly gardens on nectarivorous birds and the plants they pollinate in the CFR would be an interesting goal for future research. I would expect such gardens to likely have a longer-term impact than supplementary nectar feeders, as well as providing several added advantages (e.g., noise pollution buffers, psychological well-being, and education) (Goddard et al. 2010; Lerman and Warren 2011; Fontana et al. 2011; Pauw and Louw 2012).

It is my hope that this dissertation will inspire further research into the effects of supplementary bird feeding on pollinator-plant systems, perhaps along the themes outlined above. Such information could influence the way people perceive the urban environment and could help inform their decisions when it comes to activities that might affect natural systems. It could also encourage responsible urban planning so that connectivity between natural vegetation fragments can be restored without placing bird-pollinated plants at an extinction risk.

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Supplementary Information: Chapter 2

Table S1.1: List of bird species observed in this study, categorized according to their feeding guild.

Feeding guild	Common species name	Scientific species name
Nectar-specialist	Cape Sugarbird	*Promerops cafer*
	Malachite Sunbird	*Nectarinia famosa*
	Orange-breasted Sunbird	*Anthobaphes violacea*
	Southern Double-collared Sunbird	*Cinnyris chalybeus*
Nectar-opportunistic	Brimstone Canary	*Crithagra sulphurata*
	Cape Bulbul	*Pycnonotus capensis*
	Cape Canary	*Serinus canicollis*
	Cape Weaver	*Ploceus capensis*
	Cape White-eye	*Zosterops virens*
	Common Waxbill	*Estrilda astrild*
	Red-faced Mousebird	*Urocolius indicus*
	Southern-masked Weaver	*Ploceus velatus*
	Speckled Mousebird	*Colius striatus*
	Swee Waxbill	*Coccopygia melanotis*
	White-backed Mousebird	*Colius colius*
	White-throated Canary	*Serinus albogularis*
	Cape Sparrow	*Passer melanurus*
	Red-winged Starling	*Onychognathus morio*
	Yellow Canary	*Crithagra flaviventris*
Non-nectarivorous	African Dusky Flycatcher	*Muscicapa adusta*
	Bokmakierie	*Telophorus zeylonus*
	Cape Batis	*Batis capensis*
	Cape Bunting	*Emberiza capensis*
	Cape Francolin	*Pternistis capensis*
	Cape Grassbird	*Sphenoeacus afer*
	Cape Robin-chat	*Cossypha caffra*
	Cape Siskin	*Crithagra totta*
	Cape Turtle Dove	*Streptopelia capicola*
	Cape Wagtail	*Motacilla capensis*
	Common Fiscal	*Lanius collaris*
	Common Starling	*Sturnus vulgaris*
	Familiar Chat	*Cercomela familiaris*
	Fiscal Flycatcher	*Sigelus silens*
	Grey-backed Cisticola	*Cisticola subruficapilla*
	Hadeda Ibis	*Bostrychia hagedash*
	Helmeted Guineafowl	*Numida meleagris*
	House Sparrow	*Passer domesticus*

Karoo Prinia	*Prinia maculosa*
Karoo Thrush	*Turdus smithi*
Klaas's Cuckoo	*Chrysococcyx klaas*
Laughing Dove	*Streptopelia senegalensis*
Neddicky	*Cisticola fulvicapilla*
Red-eyed Dove	*Streptopelia semitorquata*
Southern Boubou	*Laniarius ferrugineus*
Southern Red Bishop	*Euplectes orix*
Speckled Pigeon	*Columba guinea*
Yellow Bishop	*Euplectes capensis*

Figure S1.1: A cluster of four plastic supplementary nectar feeders were placed in the gardens. Each pair of feeders was mounted on a stick attached perpendicularly to an iron rod recessed into the ground. Birds perch on the sticks as they await their turn to feed. The see-through bottles, through which it is easy to monitor solution levels, were filled with a colourless 1:4 sugar to water solution and then attached to a red platform. The solution is channelled towards three feeding holes in the platform, equally spaced from one another, large enough for larger-beaked nectar-opportunistic species to access the solution. A perch is located at each feeding hole to allow birds to rest comfortably as they feed.

Table S1.2: Type of error distribution used in the models for each of the three feeding guilds and for the nectar-specialist species. An information theoretic approach was used to select the most appropriate error distribution for each dataset based on the difference between the Akaike Information Criterion. I fitted and compared Poisson, negative binomial, zero-inflated Poisson (ZIP) and zero-inflated negative binomial (ZINB) distributions. nbinom2 is a negative binomial distribution in which the variance increases quadratically with the mean, while nbinom1 has a variance that increases linearly. Observation-level random effects (OLRE) were included in Poisson models to correct for overdispersion. All models assumed the log-link function.

Dataset	Poisson	ZIP	nbinom1	nbinom2	ZINB	OLRE
Nectar-specialists	✓					✓
Species-specific	✓					✓
Nectar-opportunists				✓		
Non-nectarivorous	✓					✓

Table S1.3: The full set of models for each of the three feeding guilds testing for the effect of supplementary nectar feeders on their local abundance and distribution along the urban edge of the Cape Peninsula. Generalized linear mixed-effect models were constructed, with site as a random factor and the log of the size of the survey areas as an offset. For each model, the number of parameters (K), log likelihood (L), Bayesian Information Criterion (BIC), difference in BIC (ΔBIC) from the best model and BIC weight (w_i) is presented.

Guild	Rank	Variables in model [a]	K	L	BIC	ΔBIC	w_i
Nectar-specialists	1	D * Treatment + D * S + T + FA + W + PF + P	12	-1548.22	3172.46	0.00	0.99
	2	D * Treatment * S + T + FA + W + PF + P	14	-1546.19	3181.07	8.60	0.01
	3	D * Treatment + S + T + FA + W + PF + P	11	-1572.96	3215.60	43.14	0.00
	4	D * Treatment + Treatment * S + T + FA + W + PF + P	12	-1571.64	3219.30	46.83	0.00
	5	D * S + Treatment + T + FA + Wind + PF + Pets	11	-1617.94	3305.56	133.10	0.00
	6	D * S + Treatment * S + T + FA + Wind + PF + P	12	-1616.71	3309.44	136.98	0.00
	7	D + Treatment + T + FA + W + PF + P	9	-1643.7	3344.41	171.95	0.00
	8	D + Treatment + S + T + FA + W + PF + P	10	-1643.69	3350.73	178.27	0.00
	9	D + Treatment * S + T + FA + W + PF + P	11	-1642.38	3354.44	181.98	0.00
	10	D + T + FA + W + PF + P	8	-1656.41	3363.50	191.04	0.00
	11	D + S + T + FA + W + PF + P	9	-1656.41	3369.83	197.37	0.00
	12	Treatment + T + FA + W + PF + P	8	-2000.87	4052.43	879.96	0.00
	13	Treatment + S + T + FA + W + PF + P	9	-2000.72	4058.46	886.00	0.00
	14	NULL (T + FA + W + PF + P)	7	-2013.9	4072.14	899.68	0.00
	15	S + T + FA + W + PF + P	8	-2013.67	4078.02	905.56	0.00
Nectar-opportunists	1	D * Treatment + S + T + FA + W + PF + P	12	-1110.64	2297.51	0.00	0.77
	2	D * Treatment + Treatment * S + T + FA + W + PF + P	13	-1109.18	2300.95	3.44	0.14
	3	D * Treatment + D * S + T + FA + W + PF + P	13	-1110.24	2303.06	5.55	0.05
	4	D + S + T + FA + W + PF + P	10	-1120.43	2304.39	6.88	0.03
	5	D + T + FA + W + PF + P	9	-1124.11	2305.4	7.89	0.02
	6	D + Treatment + S + T + FA + W + PF + P	11	-1118.97	2307.82	10.31	0.00
	7	D + Treatment + T + FA + W + PF + P	10	-1123.11	2309.75	12.24	0.00
	8	D + Treatment * S + T + FA + W + PF + P	12	-1117.19	2310.62	13.11	0.00
	9	D * S + Treatment + T + FA + W + PF + P	12	-1118.16	2312.54	15.04	0.00
	10	D * Treatment * S + T + FA + W + PF + P	15	-1108.87	2313.03	15.53	0.00
	11	D * S + Treatment * S + T + FA + W + PF + P	13	-1116.7	2315.99	18.48	0.00
	12	Treatment + T + FA + W + PF + P	9	-1237.8	2532.77	235.26	0.00

	13	Treatment + S + T + FA + W + PF + P	10	-1236.46	2536.45	238.94	0.00
	14	NULL (T + FA + W + PF + P)	8	-1243.78	2538.38	240.87	0.00
	15	S + T + FA + W + PF + P	9	-1243.15	2543.48	245.97	0.00
Non-nectarivores	1	D + S + T + FA + W + PF + P	9	-984.94	2026.06	0.00	0.83
	2	D * S + Treatment + T + FA + W + PF + P	11	-980.83	2030.33	4.27	0.10
	3	D + Treatment + S + T + FA + W + PF + P	10	-984.93	2032.29	6.24	0.04
	4	D * Treatment + D * S + T + FA + W + PF + P	12	-979.13	2033.17	7.11	0.02
	5	D * Treatment + S + T + FA + W + PF + P	11	-983.12	2034.9	8.84	0.01
	6	D * S + Treatment * S + T + FA + W + PF + P	12	-980.83	2036.57	10.52	0.00
	7	D + Treatment * S + T + FA + W + PF + P	11	-984.93	2038.53	12.48	0.00
	8	D * Treatment * S + T + FA + W + PF + P	14	-976.72	2040.84	14.78	0.00
	9	D * Treatment + Treatment * S + T + FA + W + PF + P	12	-983.12	2041.14	15.09	0.00
	10	D + T + FA + W + PF + P	8	-1077.1	2204.14	178.08	0.00
	11	D + Treatment + T + FA + W + PF + P	9	-1076.84	2209.87	183.81	0.00
	12	S + T + FA + W + PF + P	8	-1123.7	2297.33	271.28	0.00
	13	Treatment + T + FA + W + PF + S + P	9	-1123.68	2303.54	277.48	0.00
	14	Treatment + S + T + FA + W + PF + P	9	-1123.68	2303.54	277.48	0.00
	15	T + FA + W + PF + P	7	-1206.31	2456.31	430.26	0.00

[a] D = Distance of survey plot from the garden (0 m, 50 m, 100 m or 150 m); Treatment = feeder or control; T = time of day (morning or afternoon); FA = floral abundance estimated as the number of bird-pollinated inflorescences in each plot; W = wind speed during survey; PF = previous feeder presence in the garden (TRUE or FALSE); P = presence of pets on the property (TRUE or FALSE); S = Season (summer or winter)

Table S1.4: The full set of models for each of the three feeding guilds testing for the effect of supplementary nectar feeders on their local abundance and distribution along the urban edge of the Cape Peninsula. Generalized linear mixed-effect models were constructed, with site as a random factor and the log of size of the survey areas as an offset. For each model, the number of parameters (K), log likelihood (L), Bayesian Information Criterion (BIC), difference in BIC (ΔBIC) from the best model and BIC weight (*w_i*) is presented.

Rank	**Variables in model [a]**	**K**	**L**	**BIC**	**ΔBIC**	***w_i***
1	D * Treatment + D * Species + T + FA + W + PF + P + S	17	-2850.94	5833.14	0.00	0.98
2	D * Treatment * Species + T + FA + W + PF + P + S	23	-2831.61	5840.81	7.66	0.02
3	D * Treatment + Species + T + FA + W + PF + P + S	14	-2920.70	5949.50	116.36	0.00
4	D * Species + Treatment + T + FA + W + PF + P + S	16	-2916.45	5956.44	123.29	0.00
5	D * Treatment + Treatment * Species + T + FA + W + PF + P + S	17	-2912.80	5956.86	123.72	0.00
6	D * Species + Treatment * Species + T + FA + W + PF + P + S	19	-2908.53	5963.76	130.62	0.00
7	D + Treatment + Species + T + FA + W + PF + P + S	13	-2990.27	6080.93	247.78	0.00
8	D + Treatment * Species + T + FA + W + PF + P + S	16	-2982.36	6088.25	255.11	0.00
9	D + Species + T + FA + W + PF + P + S	12	-3003.46	6099.58	266.43	0.00
10	D + Treatment + T + FA + W+ PF + P + S	10	-3081.51	6240.23	407.08	0.00
11	D + T + FA + W + PF + P + S	9	-3094.56	6258.61	425.46	0.00
12	Treatment + Species + T + FA + W + PF + P + S	12	-3348.30	6789.26	956.11	0.00
13	Species + T + FA + W + PF + P + S	11	-3361.93	6808.79	975.65	0.00
14	Treatment + T + FA + W + PF + P + S	9	-3439.28	6948.04	1114.90	0.00
15	NULL (T + FA + W + PF + P + S)	8	-3452.71	6967.19	1134.05	0.00

[a] D = Distance of survey plot from the garden (0 m, 50 m, 100 m or 150 m); Treatment = feeder or control; Species = species of nectar-specialist bird (Malachite Sunbird, Cape Sugarbird, Orange-breasted Sunbird, or Southern Double-collared Sunbird); T = time of day (morning or afternoon); FA = floral abundance estimated as the number of bird-pollinated inflorescences in each plot; W = wind speed during survey; PF = previous feeder presence in the garden (TRUE or FALSE); P = presence of pets on the property (TRUE or FALSE); S = Season (summer or winter)

Table S1.5: Results from the best fitting model for each feeding guild after model selection to determine which variables best predict bird abundance for nectar-specialists, nectar-opportunists and non-nectarivorous bird species along the urban edge of the Cape Peninsula. The Parameter Estimates, lower limits (LL) and upper limits (UL) of the 95% confidence intervals (CI), standard error (SE), Z-values, *P*-values and variance inflation factors (VIF) for each variable are provided here. Significant *P*-values are highlighted in bold.

			95% CI					
Guild	**Variable**	**Estimate**	**LL**	**UL**	**SE**	**Z**	***P***	**VIF**
Nectar-specialists	Intercept	-6.500	-6.900	-6.090	0.20	-32.12	**0.000**	
	Distance	-1.430	-1.630	-1.240	0.10	-14.60	**0.000**	1.04
	Treatment (control)	-0.230	-0.440	-0.020	0.11	-2.18	**0.029**	1.01
	Season (winter)	0.250	-0.050	0.550	0.15	1.61	0.108	2.01
	Time (morning)	0.490	0.250	0.730	0.12	4.02	**0.000**	1.28
	Floral Abundance	0.070	-0.040	0.190	0.06	1.23	0.217	1.21
	Wind	-0.240	-0.400	-0.070	0.08	-2.86	**0.004**	2.15
	Previous Feeder (TRUE)	-0.450	-0.900	-0.010	0.21	-2.12	**0.034**	1.01
	Pets (TRUE)	-0.004	-0.450	0.440	0.21	-0.02	0.987	1.01
	Distance:Treatment (control)	0.650	0.430	0.870	0.11	5.86	**0.000**	
	Distance:Season (winter)	0.340	0.120	0.560	0.11	3.01	**0.003**	
Nectar-opportunists	Intercept	-5.536	-5.989	-5.082	0.23	-23.92	**0.000**	
	Distance	-1.444	-1.620	-1.269	0.09	-16.11	**0.000**	2.17
	Treatment (control)	-0.176	-0.455	0.102	0.14	-1.24	0.214	1.42
	Season (winter)	-0.655	-1.059	-0.251	0.21	-3.18	**0.001**	2.18
	Time (morning)	-0.141	-0.443	0.161	0.15	-0.92	0.360	1.26
	Floral Abundance	-0.254	-0.452	-0.055	0.10	-2.50	**0.012**	1.17
	Wind	-0.252	-0.463	-0.042	0.11	-2.35	**0.019**	2.29
	Previous Feeder (TRUE)	-0.097	-0.531	0.337	0.22	-0.44	**0.662**	1.00
	Pets (TRUE)	-0.378	-0.807	0.051	0.22	-1.73	0.084	1.01
	Distance:Season (winter)	0.511	0.267	0.754	0.12	4.11	**0.000**	
Non-nectarivores	Intercept	-6.156	-6.214	-5.683	0.16	-38.47	**0.000**	
	Distance	-0.839	-0.834	-0.654	0.07	-12.41	**0.000**	1.02
	Season (winter)	-1.501	-1.669	-1.233	0.18	-8.26	**0.000**	1.84
	Time (morning)	0.057	-0.176	0.155	0.14	0.40	0.692	1.23
	Floral Abundance	-0.040	-0.127	0.084	0.08	-0.51	0.610	1.15
	Wind	-0.340	-0.495	-0.267	0.09	-3.66	**0.000**	1.96
	Previous Feeder (TRUE)	-0.210	-0.467	0.168	0.13	-1.56	0.119	1.02
	Pets (TRUE)	-0.467	-0.680	-0.042	0.14	-3.41	**0.001**	1.03

Table S1.6: Results from the best fitting model after model selection for the nectar-specialist species to determine the effect of nectar feeders on the abundance and distribution of all four species along the urban edge of the Cape Peninsula. The Parameter Estimates, lower limits (LL) and upper limits (UL) of the 95% confidence intervals (CI), standard error (SE), Z-values and *P*-values are provided here. Significant *P*-values are highlighted in bold. MS = Malachite Sunbird; OBS = Orange-breasted Sunbird; SDC = Southern Double-collared Sunbird.

		95% CI				
Variable	**Estimate**	**LL**	**UL**	**SE**	**Z**	***P***
Intercept	-8.17	-8.48	-7.88	0.15	-53.51	**0.000**
Distance	-1.30	-1.50	-1.10	0.10	-12.63	**0.000**
Treatment (control)	-0.28	-0.45	-0.10	0.09	-3.04	**0.002**
Species (MS)	-0.75	-1.02	-0.48	0.14	-5.47	**0.000**
Species (OBS)	0.40	0.17	0.63	0.12	3.34	**0.001**
Species (SDC)	-0.27	-0.52	-0.02	0.13	-2.11	**0.035**
Time (morning)	0.48	0.28	0.67	0.10	4.77	**0.000**
Floral Abundance	0.14	0.06	0.23	0.05	3.22	**0.001**
Wind	-0.17	-0.30	-0.04	0.07	-2.63	**0.009**
Previous Feeder (TRUE)	-0.40	-0.58	-0.21	0.09	-4.21	**0.000**
Season (winter)	0.15	-0.09	0.40	0.12	1.23	0.218
Pets (TRUE)	0.06	-0.12	0.24	0.09	0.62	0.533
Distance:Treatment (control)	0.73	0.54	0.92	0.10	7.64	**0.000**
Distance:Species (MS)	-0.31	-0.60	-0.03	0.15	-2.16	**0.031**
Distance:Species (OBS)	0.46	0.22	0.71	0.12	3.72	**0.000**
Distance:Species (SDC)	-0.42	-0.69	-0.16	0.13	-3.15	**0.002**

Supplementary Information: Chapter 3

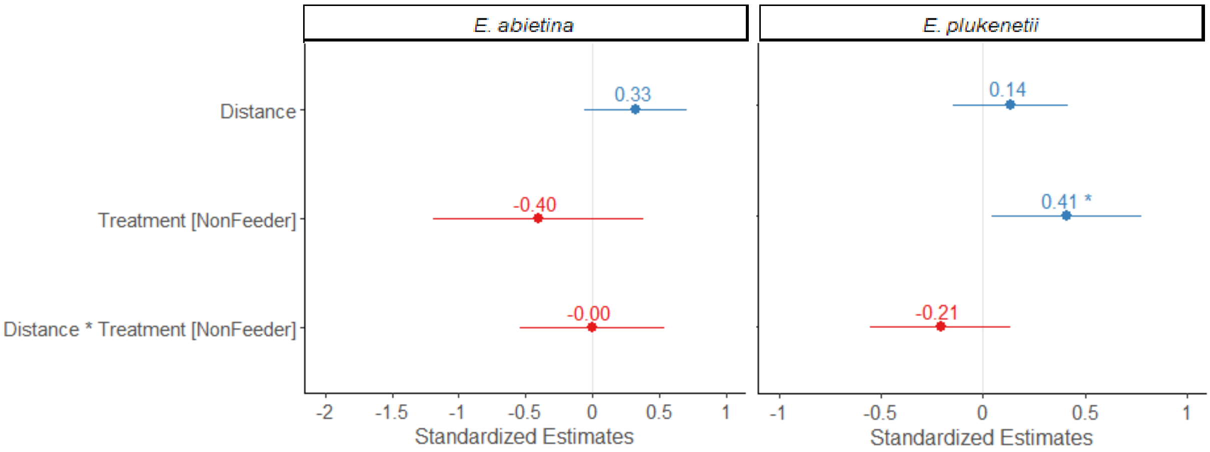

Figure S2.1: Forest-plot of the standardized estimates with 95% confidence intervals (CI) for the variables in the linear mixed-effects models, indicating the strength of their effects. The standardized estimates capture how many standard deviations visitation rate will change per standard deviation increase in the predictor. Only nectar feeder presence, not distance from feeders, affected *Erica plukenetii* pollinator visitation. None of the predictor variables influenced *E. abietina* visitation (CI's overlap zero).

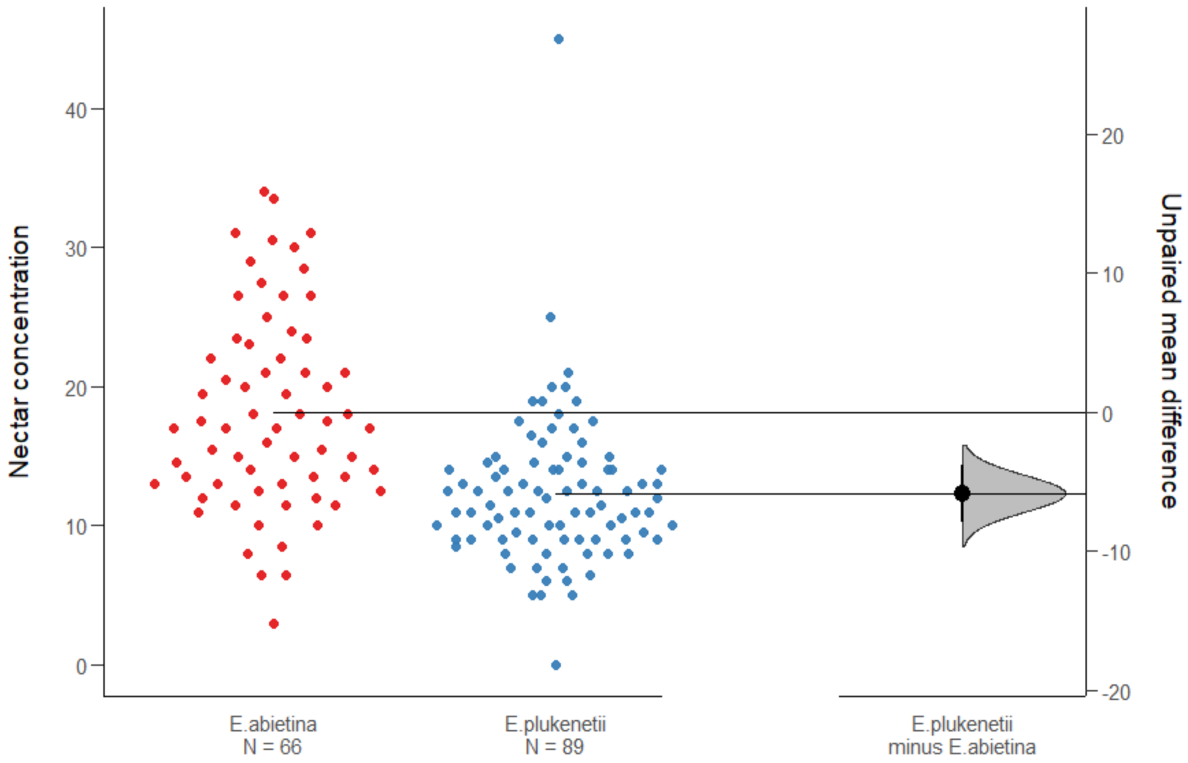

Figure S2.2: Estimation plot of the difference in floral nectar concentration (weight/weight) between *Erica plukenetii* and *E. abietina* in Cape Point, near the study area for this study, during May – September 2016. (Left) Raw datapoints presented in a swarmplot. (Right) Effect size as the mean difference in nectar concentration between *Erica* species (black dot) with its resampled distribution given the observed data (grey curve) and 95% confidence interval (vertical bars). The average nectar concentration for *E. abietina* flowers is significantly greater than for *E. plukenetii* (-5.85, 95% CI [-7.89; -3.82]). I produced the estimation plot using the dabestr package (Ho et al. 2019).

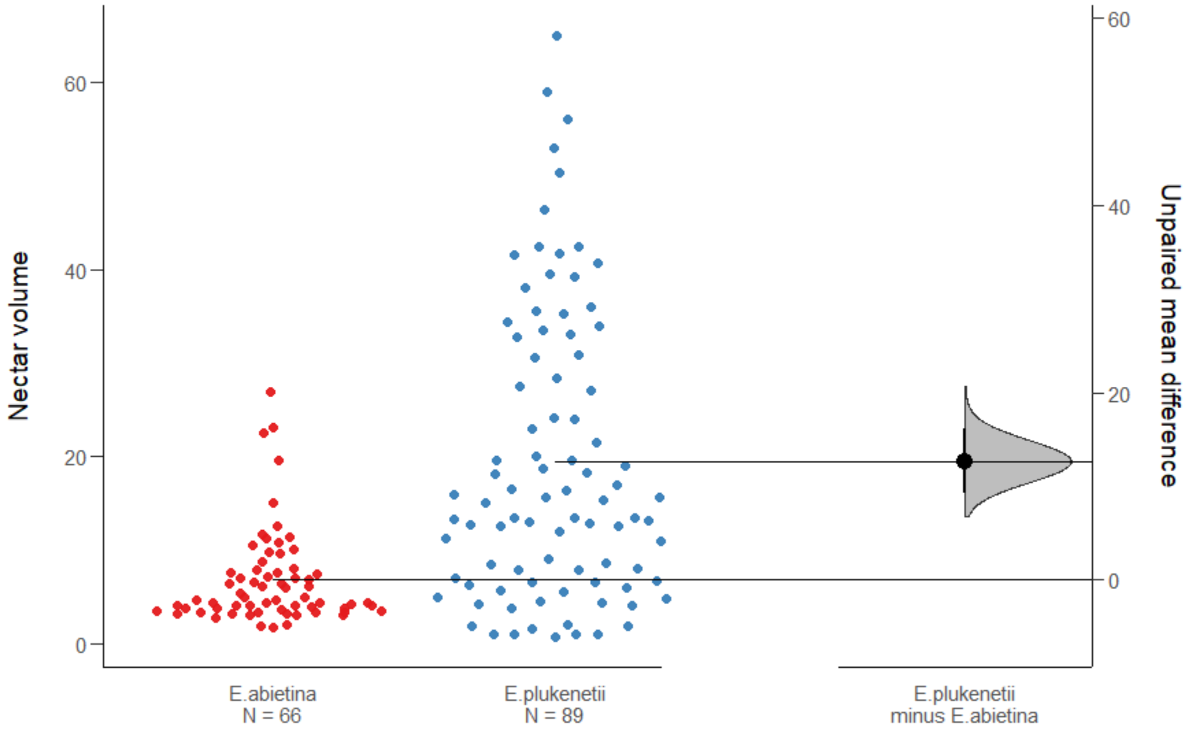

Figure S2.3: Estimation plot of the difference in nectar volume between *Erica plukenetii* and *E. abietina* flowers in Cape Point, near the study area for this study, during May – September 2016. (Left) Raw datapoints presented in a swarmplot. (Right) Effect size as the mean difference in nectar volume between *Erica* species (black dot) with its resampled distribution given the observed data (grey curve) and 95% confidence interval (vertical bars). The average nectar volume for *E. abietina* flowers is significantly lower than for *E. plukenetii* (12.7, 95% CI [9.28; 16.1]). I produced the estimation plot using the dabestr package (Ho et al. 2019).